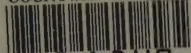


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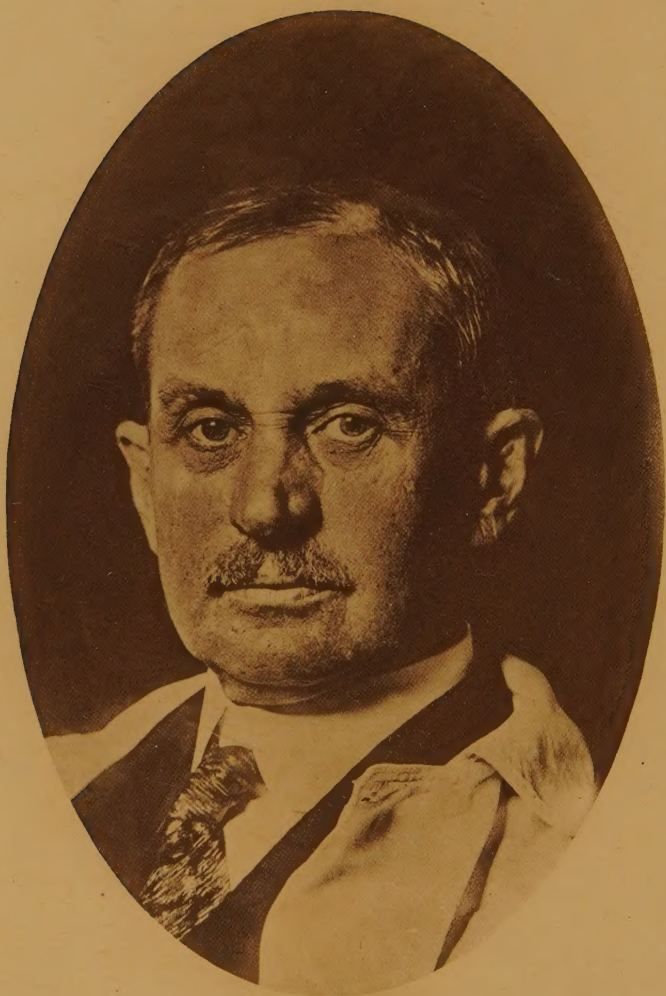
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J.P. Mau



FRANKLIN PAINE MALL

1862-1917

IN MEMORIAM

This hour, of our busy session, has been set aside to enable us to voice our deep appreciation, our gratitude and affection of one who has been wont to meet with us, one of our members whose busy and eventful life, but recently and all too suddenly was brought to an end. On November 17 we were shocked and grieved to learn of the death of Franklin Paine Mall, Professor of Anatomy at Johns Hopkins University and Director of the Department of Embryology of the Carnegie Institution of Washington. We who in thought lingered at his bedside during the final week of illness, though separated by boundaries of states, we who were made hopeful or sorrowed as bulletins were received, and were in a measure led to anticipate the end, were none the less unprepared to sustain the grief which came with the realization of the sudden ending of a career which has meant so much to the development of scientific Anatomy in America. On this 17th day of November there came to a close the lives of two notable personalities with international standing. The one, Auguste Rodin, with years numbering more than three score and ten, who labored more than half a century to reach fame, one whose molded clay and chiseled stone expressed structure and movement; the other, our departed member, who in the scarce more than half century of life, obtained a commanding position early in his career and of his brief span was for nearly a quarter of a century recognized at home and abroad as an able investigator, with wide sympathies, and keen and broad vision; one who saw life in a dead section; one who has been teacher to many of us though we held not the formal relation of pupils.

An address, in memory of Franklin Paine Mall, presented at the thirty-fourth session of the American Association of Anatomists, convened at the University of Minnesota, December 27 to 29, 1917.

We are at the moment too near to sorrow to sketch with full justice this life. I have been the more willing to give expression to our feelings, at this time, since I fully realize that no word of eulogy of mine is needed to bring him to your appreciation. We are all familiar with the results of his labor. To nearly all of us there has been a personal side, not revealed in printed page. To me, he has been a helpful friend of many years standing, one whose frank though kindly criticism as well as encouraging word, whether written or spoken, have been appreciated and have influenced my endeavors and will influence them to the end of my labors.

Franklin Paine Mall was born September 28, 1862, on a farm some two miles distant from Belle Plaine, Iowa, the son of Francis and Louise (Miller) Mall. His father came to America from Germany in 1848. His mother, born in this country, died during his early boyhood. His preliminary education was received largely at a boarding school situated near his home. He entered the Department of Medicine and Surgery of the University of Michigan, apparently on the advice of their family physician, who had graduated there, in the autumn of 1880, and received the degree of Doctor of Medicine from this institution on June 28, 1883; thus several months before attaining majority. This period of study fell to a time when "The Faculty recognizes what is evident in the experience of all medical students, that attendance upon lectures on the same subject a second time, is much more interesting and profitable than the first; hence they require students to attend lectures on all the leading subjects more than once." Probably speaking from his own experience—Liberty in Medical Education—he states "When the third year course was introduced the second year was the first year taken over again, with a special third year course added. In this way the student heard each course of lectures twice in order to make him remember it." Laboratory courses in anatomy and histology were required, though in later years while discussing the need of careful work in the dissecting room, with reference to the value of Barker's Manual, he states that "Nowhere do we read that the 5000 questions which were

placed before me while a medical student give the 'royal road' to knowledge." It is stated that instead of taking lectures over again, yes a first time in certain courses, this medical student chose the alternative of study in the library. Of his then teachers he has spoken to me of two—Vaughan and Sewall—as having given inspiration and incentive to further work. To me, who approached this same course at about the same age and with essentially the same preliminary training and only a few years later, retrospect does not reveal much specific knowledge gained during undergraduate days; rather one had opportunity to acquire an attitude of mind. A 'trieb' within for knowing the unknown did find congenial environment in the quiet and stimulating University atmosphere, with approach to academic ideals.

The years immediately following graduation in medicine, Doctor Mall spent in study in Europe. The first year (1884) at Heidelberg, where he pursued various medical subjects, lived the life of a student and perfected himself in the German language. In his discussion of liberty in medical education, with special reference to sequence or courses, we read "If a student desires to take pathological histology without having had normal histology and the instructor did not object, the student would have to take the consequences. I myself did this as a student at Heidelberg and to this day I have not regretted it." The years of 1885-86 were spent in Leipzig and the greater part of this time in Ludwig's laboratory, and he was profoundly influenced by this teacher, one whom Minot has characterized "as the greatest teacher of the art of scientific research whom he had ever met." The influence of Ludwig was the dominant one in molding his future scientific ideals as well as his attitude toward medical education. The happy relations existing in the laboratory between Ludwig and his pupils was one which impressed him greatly and was emulated by him in his own laboratory in later years. During his second year at Leipzig a part of the time was spent in study in the laboratory of His. This great teacher of anatomy was not so congenial and less approachable. In his account of the life of Wilhelm His he informs us that "When

I knocked at his door at first I was turned away, but after appearing a number of times I was finally accepted." Teacher and pupil became intimate friends in later years. Doctor Mall spent many summers in Leipzig working with His. Their intimacy was based on common interests in similar scientific problems. The clear reasoning and direct manner of formulating and solving problems, characteristic of His, impressed and influenced his pupil and co-worker. The results of his two years of study at Leipzig are embodied in two publications, one from each of the two laboratories in which his special work was carried on—"Die Blut-und Lymphwege im Dünndarm des Hundes" and "Entwicklung der Branchialbogen und Spalten des Hühnchens," characteristic of the spirit of the two laboratories and in a measure foreshadowing the main lines of his future work.

On his return to America Doctor Mall was called to Baltimore, where he entered upon the duties of Fellow in Pathology, under Professor Welch (1886-88) in association with Doctors Halstead and Councilman. He was named Instructor in Pathology, 1888-89. These were further years of training, devoted to investigation, as attested by a number of publications. It is deemed fitting to emphasize here this long period of training devoted to research, and the breadth of the training—physiology, embryology and pathology. Doctor Mall has often, in spoken and written word, stressed the necessity of training in research as a preparation for an academic career and has pled for the opportunity for such training in our American Medical Schools. "In America," he writes, "we frequently find recent graduates who tell us they would follow an academic career if their future were assured as far as salary is concerned. Little do they realize that this attitude of mind alone would exclude them absolutely from such a career."

With the opening of Clark University Doctor Mall became Adjunct Professor of Vertebrate Anatomy (1889-92), and with the foundation of Chicago University, Professor of Anatomy (1892-93). With the establishment of the School of Medicine at Johns Hopkins University, he returned to Baltimore to enter upon the duties of Professor of Anatomy and Director of the

Laboratory, which position he held at the time of his death, assuming in 1914, in conjunction, the directorship of the newly created Department of Embryology of the Carnegie Institution of Washington. The University of Michigan honored him and honored itself by conferring the degree of A.M., in 1900, and the degree of Sc.D., in 1908. He received the degree of LL.D., from the University of Wisconsin, in 1904. His sympathies in the sciences, more particularly in the Biological sciences were broad, and in an advisory capacity, as a member of committees or of boards, he did much to promote his chosen and allied sciences. He was sometime a trustee of the Woods Hole Biological Laboratory, member of the Advisory Board of The Wistar Institute, member of the committee of brain research of the International Association of Academies, member of the National Academy of Sciences, of the American Philosophical Association, Fellow of the College of Physicians of Philadelphia and member of many learned societies of America.

Doctor Mall's publications number somewhat over one hundred. Time does not permit, nor is this the opportunity to present a bibliographic list and discuss critically these publications. This I am attempting for record elsewhere. However, a fleeting survey may here be permitted. His Leipzig teachers, Ludwig and His, were sometime teachers both of anatomy and physiology and many of Ludwig's researches were of physiological problems studied chiefly on an anatomical basis, bringing structures and course of blood vessels in relation with function of organs. This functional or physiological anatomy is exemplified in his studies of the blood and lymph vessels of the dog's small intestine and stomach, his studies of the spleen lobule, and of the structural unit of the liver. Finished contributions of studies in which methods of vascular injection, corrosion injection, maceration and differential digestion were used to advantage in reaching definite conclusions. Of his more purely physiologic researches may be mentioned the studies of the vasomotor supply of the Portal System. His careful and illuminating studies of the histogenesis of the connective tissue from mesenchymal syncytium and of collagenous, yellow

elastic and reticular fibrils have given us a new conception of the structure of connective tissue. However, from the time of his early studies in embryology in the His laboratory, resulting in his first publication, embryology and histogenesis have been the chief theme of his investigation, his real program for modern anatomy. The embryological studies contributed by himself, with many others emanating from his laboratory, have greatly extended the bounds of our knowledge of developmental processes, especially as concerns the human embryo, the development of which, except for earliest stages, is now better understood than that of any other mammal, and this largely through his labors, his coöperation or his incentive. Doctor Mall's first embryological contribution dealt with the development of the branchial cleft region of the chick, followed in close succession by a series of studies of this region, both in chick and mammals. These were followed by a series of papers on the development of the coelomic cavity, culminating in his well known contribution to the development of the human coelom. His study of a human embryo 26 days old, falling to the early period of his work (1891) exemplifies a characteristic of the embryological work of His, namely, that he viewed the embryo as a whole and carried the investigation to its logical conclusion. This study has been the prototype for other investigations of human and other mammalian embryos. The contribution to the development of the human intestine and its position in the adult exemplifies another type of embryological work, one worthy of special commendation. Of it, His has stated in a private letter—"What is lacking in the majority of contributions to embryology is a fundamental conception of the transition phases from early developmental stages to fetal and adult stages. For the intestine you have now completed this chain, from beginning to end, and this I hold to be a great advance." This broad conception of embryologic investigation characterizes other of his contributions; his studies on the development of the heart, normal and pathological, and of the structure of the adult heart, his studies of the structural unit of the liver, of the blood vessels of the brain and other vessels, all bring to conclusion developmental stages and

give the key to modern anatomic investigation. With the increase in the size of the human embryological collection at Johns Hopkins University, the need of determining more definitely the age relation to the size of the human embryo, the sequence of stages and a uniform and well authenticated designation of stages, became apparent, and much thought was given this phase of embryologic investigation. The results of these reflections have appeared in a number of publications which have proven essential and helpful in the correlation of investigations on the human embryo. The ever-growing collection of human embryos contained many specimens of pathologic ova and young embryos, which have formed the basis for a number of monographic contributions dealing with the pathology of early human embryos, the causes underlying the origin of human monsters, of cyclopia in the human embryo, the frequency of localized anomalies in human embryos and infants at birth, the causes of tubal pregnancy and the fate of the embryo in tubal pregnancy. Much of this later work was pioneer work and of the greatest value; of interest not only to the specialist but of a wide general interest. The "Manual of Human Embryology," edited by Keibel and Mall, and published simultaneously in German and in English, marks a milestone in the progress of our knowledge of human development and embodies the crystallized thought of Doctor Mall and his co-workers.

Doctor Mall was for many years vitally interested in the question of medical education. From the time of his early Leipzig days, influenced by the attitude existing between Ludwig and his pupils, influenced also by this able investigator's views on medical education and on university education in general, he agitated for more liberty in medical education. "How different is the study of medicine in Europe than in America. There freedom reigns and students wander from place to place, being controlled only by a fairly rational system of examinations in case they wish to graduate," we hear him say. And again—"Liberty to the student should not mean license to him, but rather liberty also to the instructor." He has argued for more liberal curricula, concentration of courses, opportunity for elec-

tives on the part of the student, but also for more freedom from routine and better facilities for research on the part of the teacher. "A medical department of a University must consist of a group of independent departments, each a complete organization in itself, existing primarily as a conservator of the branch it represents. Teaching beginners may become its chief work, but should never be its chief ideal." I am not prepared to say just how much of the improvement in medical education witnessed during the past decade is due to his influence, direct or indirect, though I feel that he has been a potent factor; and may we come to a nearer realization of his ideals.

His chief concern was of necessity with departments of anatomy. On entering upon the real work of his life, at Johns Hopkins University, he was able to organize a department of anatomy unhampered by traditions, and in an environment of academic freedom, surrounded by departments devoted to scientific research, he was able, from the beginning, to realize certain of his ideals. The work of the department was placed on a broad basis. "To bring about desired reform it is necessary to have represented in an anatomical department, even in a medical school, all which naturally belongs to this science. The study of anatomy begins with the cell, ends with the entire individual, and includes man," we were informed in his remarks to this association as president. And again—"A subject like anatomy, taught for many centuries, has recently been made a new science through the studies in embryology and histology." His was the first department of anatomy in America in which all divisions of anatomy were thus correlated, not alone in printed announcement but in daily practice. Other medical schools have followed, but some have been tardy followers. From the beginning much needed reform was instituted in the dissecting room; his was not a 'dissecting room' but a laboratory. Consideration was given to adequate preservation of material. The aim from the beginning was to make the study of anatomy inductive, and a type of instruction in gross anatomy was inaugurated and carried on with eminent success, which if followed by many of us would inevitably have cost us our positions.

The student was led to make a complete dissection, using atlases, text-books and manuals. Analyzing the object itself was thought to be of infinitely more value than watching the results exposed by another. Neat, careful and accurate dissection was insisted upon, for it was appreciated that "The thorough dissector is much more likely to become a fine and discriminating physician and an effective and progressive surgeon." And further—"The importance of working out the finer structure lies not always so much in the actual knowledge gained by the student, as in the acquisition of the habits of thoroughness of observation and investigation." Such a course in gross anatomy could only be carried on in a department the staff of which was actively engaged in scientific research and in contributing to the progress of anatomy. From the beginning and through these many years he has been able to associate with himself a corps of able assistants and co-workers, who have profited by his methods and acquired his ideals, and many of them have become able and independent investigators. It was fortunate that when reorganization of medical schools became imperative, and full-time and trained teachers were sought, this need for the departments of anatomy was met, and in a number of medical schools the departments of anatomy formed the nucleus around which reorganization was effected. May I be permitted to quote from the English periodical *Nature* (February 3, 1916) in which the reorganization of embryological research in America, and incidentally its departments of anatomy, are considered; and I quote with full accord—"Five-and-twenty years ago anatomists in America were British in method and spirit; they were easy-going, each man following leisurely his own individual bent. Since that time a remarkable change has taken place; the number of laboratories in which the structure and development of the human body are taught and investigated have increased tenfold; the number of investigators has grown in a still greater ratio; in quantity and quality their anatomical proceedings and journals have come to rival those of any country in Europe. In effecting this transformation the chief credit must be assigned to one man—Franklin P. Mall, for twenty-three years professor of anatomy

at the Johns Hopkins University. He planted in Baltimore the methods and aims which he acquired when working in the laboratory of the late Professor His at Leipzig. By his personal influence and example, by pupils and disciples, and by reason of the inherent excellence of the Leipzig traditions, he has succeeded in Germanizing the majority of the dissecting rooms and anatomical laboratories throughout the length and breadth of North America." I never entered the unpretentious little building, situated at the corner of Wolfe and Monument Streets, though admirably planned within, crowded to the doors, with walls of halls covered with drawings of illustrations of contributions to all phases of anatomy, nor shared the simple noon-hour lunch of staff, perhaps each contributing to my share, without realizing to the full, that not brick and mortar, not even chiseled stone adorned by marble, make an anatomic institute.

During the early period of the regeneration of anatomic departments in our medical schools, the need of a medium for publishing in America, contributions to anatomy emanating from American laboratories, was keenly felt by him. Scientific anatomy had been wrested from the medical school by collegiate and University departments of Zoology; the scattered contributions to anatomy were being published abroad or in our own journal devoted primarily to Zoology or to general science. And, while he believed fully in the catholicity of the Biological Sciences, he did not like to have it said of our association that its prominent members were not anatomists but biologists or something else. To enable fuller expression of anatomic thought, to assist in developing and differentiating work in the anatomic laboratories of our medical schools, and the creation of a science of anatomy in America, The American Journal of Anatomy was founded. The realization of the need was largely his. In the fruition of the plans, an editorial board drawn from workers in a number of laboratories was created. Members of this board, laboratories and others interested in the development of anatomy, subscribed a sufficient fund to assure the publication of the early volumes. The journal at once became the organ of this association; membership in it automatically giving subscription to the

journal. The early volumes were edited and published from his laboratory. The high standard set for contributions accepted, the enthusiasm with which the work was carried on, the sacrifice of time given to the work by himself and associates in his laboratory, did much to insure the success of this journal. After the issuance of the first few volumes of *The American Journal of Anatomy*, a few pages were set aside in each number, under the heading of "Anatomical Record." To these pages he contributed freely himself; and nearly always, whether in book review, in record of collection or brief note, the dominant theme pertains to development of anatomy. The *Anatomical Record*, which thus had its anlage by budding, soon developed into an independent organ, which has differentiated with the development of anatomy. With the re-formulation of the aims of The Wistar Institute of Anatomy under the directorship of Doctor Greenman, who, with far-seeing policy, appreciated the opportunity of lending the aid of this Institute to the development of scientific anatomy in America, and with full approval of an Advisory Board of Anatomists for this Institute, created at his suggestion, the publication office of *The American Journal of Anatomy* and *The Anatomical Record*, and other prominent morphologic journals, was transferred to The Wistar Institute. To the wisdom of establishing and maintaining these relations we can all testify. It has seemed to me that there has been no one effort on the part of The Wistar Institute which has been so instrumental in developing scientific anatomy in America as the broad policy shown by its Director in furthering the interests of our anatomic publications. We anatomists acknowledge a debt to the Director of this Institute as well as to Doctor Mall; the realization of the need of an American journal of Anatomy, and the appreciation of its value in furthering the development of scientific anatomy in our medical schools, to a large measure its inception and an ever present help in earlier stages of development, we owe to the one; the other through material aid and broad policy has been instrumental in bringing to fuller fruition the earlier endeavors.

It is peculiarly fitting and appropriate that an appreciation of the life and influence of Doctor Mall should be presented at a

session of the American Association of Anatomists. Some time its President and for a large number of years member of its executive committee, ever interested in its welfare and keenly appreciative of its growth in numbers and influence and ever appreciating character of papers and demonstrations presented at its yearly sessions; to him this expressed growth of anatomy in America. Three years ago, this association assembled in its thirty-first session recorded in resolution its profound sense of sorrow and deep feeling of the loss sustained by the death of Charles Sedgwick Minot, he having died the 19th of November preceding. We recorded in appropriate words our appreciation of his labors in furthering the affairs of this association. I recall distinctly a session of this society, held in New Haven some twenty years ago, one of the first I attended. This session marked the turning point in the growth and development of our association. Plans for reorganization were then instituted. At a subsequent meeting, Professor Huntington was elected to the presidency, which office he held for a period of four years, important years in our evolution. I became your secretary during this period and was permitted to come in closer official connection, and to serve in this capacity, during the terms of presidency of three of our members who more than others were responsible for the reforming of the aims and ideals of our society: Huntington, Minot, Mall. I recall the many letters received from Doctor Mall during this period, full of discussion of plans for furthering our common interests and elevating our ideals, with ever-growing lists of names proposed for new members, with plans and suggestions for furthering the development of our journals and their relation to our membership. In all ever striving with unselfish devotion and sacrifice of time, for the furthering of the affairs of this association, and thus developing scientific anatomy in America.

Perhaps the crowning work of the career of Doctor Mall, though we judge it now only in its inception, is the work connected with the Department of Embryology of the Carnegie Institution of Washington. An institute of this kind, finally achieved, was in his mind years before it was realized. He was

much impressed and influenced by a paper published by His as early as 1886, on the necessity of Research Institutes. Later when opportunity presented itself His made a plea for a research institute in neurology and one for human embryology. In answer, the commission for brain research was sanctioned by the Associated Academies. Concerning the development of plans for the research in human embryology I abstract as follows from Doctor Mall's plea for such an institute, published but a few years ago. The second project of His was referred by the Associated Academies to the Anatomic Societies for consideration, and in consequence, the German Anatomic Society, in the meeting of 1901, appointed a committee to arrange for coöperation in embryologic research; it developed no activities. Not until the time of the Brussels meeting of the Anatomic Congress in 1910, were further definite steps taken. At that time, and as I recall at the suggestion of Doctor Minot, a committee was appointed to revise embryonic nomenclature. Shortly after this Brussels meeting a self appointed committee of three met at Utrecht to arrange for an international institute for comparative embryology. The object of the Brussels committee was to revise embryologic nomenclature and of the Utrecht conference, to make extensive collections of embryos of all vertebrates, neither committee purposed to confine its field especially to human development. Recognizing the fact that in the study of human development there are specific problems of great scientific and practical value, which cannot possibly be studied to best advantage without more concentration of energies than either the above committees had planned, and the further fact, that the science of anatomy, which in a great measure has been the mother of all biological sciences, needs a thorough revision and a new basis, to be obtained through the study of embryology, the original plan of His was again revised and ably and clearly put forth in "A Plea for an Institute of Human Embryology." Through cooperation of those especially interested, and the hearty endorsement of the late Professor Minot, this oft expressed wish was realized through the generosity and foresight of the Director and the Trustees of the Carnegie Institution of Wash-

ington, and for this recognition of anatomy in America, on the part of this Institution, we anatomists are placed in a deep and lasting obligation. The new department of embryology was stationed at Baltimore with Doctor Mall as its director. The scope of the plans for the new Institute of Human Embryology, as outlined in the plea for its creation, and already in part realized, is broad and comprehensive. It calls for a large collection of embryos, a competent staff, the very best material equipment and an appreciation of all the problems which bear on anatomy—physical anthropology, comparative embryology, physiology of gestation, pathology and teratology. The larger questions to be given consideration are—curve of growth; anatomy of various stages; morphology of the brain; histogenesis; causes of abortion; the study of monsters and of moles; comparative and experimental embryology to elucidate human. Nearly twenty subdivisions of these larger questions are enumerated and discussed. I gather from a recent report that the collection of human embryos consists of about 2000 specimens, many of which have been prepared in permanent serial sections. The collection is already unique, both in magnitude and importance, and vigorous efforts are being made to increase it, but I note also, that the chief function of an institute of human embryology is not the making of a collection, but the formulation and solution of problems. That this new institute was already at work, and the manner in which it was to fulfil its destiny, is attested by the "Contributions to Embryology," published by the Carnegie Institution, some twenty of which have appeared in monographic form, with a goodly number of smaller publications which have appeared in our Anatomic journals. May the personality and strength and the high scientific ideals of the late Director of this new Institute for the study of human embryology serve as an example and stimulus to such as follow in his footsteps; we conceive of no surer avenue to success.

Such has been his life; here briefly, all too briefly and I realize inadequately told. I cannot leave its appreciation without referring to the loving care and affectionate solicitude with which it has been watched over by his trusted wife. Who, trained in

anatomy, was fully appreciative of his endeavors and ever interested in the development and realization of his ideals. We who have been permitted to partake of the kindly and sincere hospitality of their home, will cherish pleasant memories. To her and to the family, we as individuals and collectively as an association, extend our most sincere and heartfelt sympathy. May the knowledge that this profound sorrow is mutually borne, lighten their grief.

In closing I make use of the opening paragraph of his account of the life and influence of Wilhelm His, his teacher and his friend—"The ancient science of anatomy has been perpetuated and extended during the many centuries of its existence by great men who have dedicated their lives to it. The list is a long one for the development of the science has been slow and progressive from the earliest ages to the present time; we find in it on the one hand, some of the greatest who have ever lived—Aristotle, Vesalius—on the other, the names of those who rank as leaders of a generation, Bichat, His." To the names of Bichat and His, I would add, with your accord, the name of Mall.

G. CARL HUBER.

PROCEEDINGS OF THE AMERICAN ASSOCIATION OF ANATOMISTS

THIRTY-FOURTH SESSION

*Institute of Anatomy, University of Minnesota, Minneapolis,
Minnesota*

December 27, 28 and 29, 1917

THURSDAY, DECEMBER 27, 10.00 A.M.

The thirty-fourth session of the American Association of Anatomists was called to order by President Henry H. Donaldson, who appointed the following committees:

Committee on Nominations for 1918: Professor Thomas G. Lee, Chairman; Professors A. G. Pohlman and W. H. F. Addison.

Auditing Committee: Professor H. M. Evans, Chairman; and Professor C. R. Bardeen.

The morning session was devoted to a symposium on "The Teaching of Anatomy and the Inculcation of Scientific Methods and Interest." Following this an address was delivered by Professor G. Carl Huber in memory of Professor Franklin P. Mall.

THURSDAY, 12.15 P.M. ASSOCIATION BUSINESS MEETING, PRESIDENT HENRY H. DONALDSON, PRESIDING.

The Secretary reported that the minutes of the Thirty-third Session were printed in full in *The Anatomical Record*, volume 11, number 6, pages 311 to 315, and read the minutes as printed. On motion, seconded and carried, the minutes of the Thirty-third Session were approved by the Association as printed in *The Anatomical Record*.

Professor Evans reported for the Auditing Committee as follows: The undersigned Auditing Committee has examined the accounts of Doctor Charles R. Stockard, Secretary-Treasurer

of the American Association of Anatomists and finds the same to be correct with proper vouchers for expenditures and bank balance on December 19, 1917, of \$303.83.

[Signed] H. M. EVANS,
C. R. BARDEEN.

The Treasurer made the following report for the year 1917:

Balance on hand December 23, 1916, when accounts were last audited.....	\$264.34
Receipts from dues 1917.....	2400.75
Total deposits.....	\$2665.09
Expenditures for 1917:	
Postage and telegrams.....	\$40.00
Printing and Stationery.....	22.70
Collection and exchange.....	1.31
Stenography-typewriting.....	41.75
Wistar Institute for subscriptions, Journal of Anatomy, Anatomical Record, etc.....	2255.50
Total expenditures.....	2361.26
Balance on hand.....	\$303.83
Balance on hand, deposited in the name of the American Association of Anatomists in the Corn Exchange Bank, New York City.	

On motion the reports of the Auditing Committee and the Treasurer were accepted and adopted.

The Secretary announced that the Committee on Nominations, through its Chairman, Professor J. P. McMurrich, places before the Association the following names: For President, Professor R. R. Bensley; for Vice-President, Professor C. R. Bardeen; for Secretary-Treasurer, Professor C. R. Stockard; for members of the Executive Committee, term expiring 1921, Professors G. S. Huntington and H. E. Jordan.

On motion the Secretary was instructed to cast a ballot for the election of the above named officers.

Dr. G. L. Streeter was elected to serve the unexpired term on the executive committee made vacant by the death of Professor Mall.

The Secretary presented the following names recommended

by the Executive Committee for election to membership in the American Association of Anatomists.

- APPLEBY, J. I., A.B., Graduate Assistant in Anatomy, *University of Missouri, Columbia, Mo.*
- BATSON, O. V., A.B., Medical student at Washington University, *Washington University Medical School, St. Louis, Mo.*
- CAMERON, JOHN, M.D., D.Sc., F.R.S.E., Professor of Anatomy, *Dalhousie Medical College, Halifax, Nova Scotia.*
- CARDWELL, JOHN C., M.D., Professor of Physiology, Long Island College Hospital, *Henry and Amity Sts., Brooklyn, New York.*
- CARTER, JAMES THORNTON, D.D.S., Research Worker, Department of Zoology, *University College, 1 Hanover Square, London, W., England.*
- CASH, JAMES ROBERT, A.B., A.M., Student of Medicine, *Johns Hopkins Medical School, Baltimore, Maryland.*
- CHAPMAN, W. B., A.B., Medical Student, *Washington University Medical School, St. Louis, Mo.*
- CONEL, JESSE LE ROY, Ph.D., Instructor in the Department of Anatomy, New York University, *338 East 26th St., New York City.*
- COOKMAN, ALFRED, A.B., Instructor in Agriculture and Biology, *Long Beach High School, Long Beach, Cal.*
- CRAIGIE, E. HORNE, A.B., Instructor in the Department of Biology, *University of Toronto, Toronto, Canada.*
- CROSBY, ELIZABETH CAROLINE, Ph.D., Principal of High School, *Petersburg, Michigan.*
- DONALDSON, JOHN C., B.S., M.D., Instructor in Anatomy, *University of Cincinnati Medical College, Cincinnati, Ohio.*
- ELWYN, ADOLPH, A.M., Assistant Professor of Anatomy, Long Island College Hospital; Hoagland Laboratory, *Henry and Pacific Sts., Brooklyn, New York.*
- EVANS, THOMAS HORACE, M.D., Associate Professor of Anatomy, Long Island College Hospital, *Henry and Amity Sts., Brooklyn, New York.*
- FORMAN, JONATHAN, A.B., M.D., Assistant Professor of Pathology, College of Medicine, Ohio State University, *Naval Hospital, Hampton Roads, Virginia.*
- GILLASPIE, C., M.D., Professor of Anatomy, *University of Colorado, School of Medicine, Boulder, Colorado.*
- GUTSELL, ROBERT S., A.B., Teaching fellow in Anatomy, *Institute of Anatomy, University of Minnesota, Minneapolis, Minn.*
- HEMLEB, WM. FRANCIS, M.D., Assistant Professor of Anatomy, *Georgetown University, Washington, D. C.*
- HINES, MARION, A.B., Instructor in Anatomy, *University of Chicago, Chicago, Illinois.*
- KITTELSON, JOHN A., B.S., A.M., Instructor in Anatomy, *University of Nebraska College of Medicine, Omaha, Neb.*
- MCJUNKIN, F. A., M.A., M.D., Professor of Pathology, *Marquette University School of Medicine, Milwaukee, Wisconsin.*
- MAGATH, THOMAS BYRD, M.S., Ph.D., Instructor in Anatomy, *University of Illinois, College of Medicine, Chicago, Ill.*

- O'DONAGHUE, CHARLES H., D.Sc., F.Z.S., Senior Assistant in Zoology and Comparative Anatomy, *University College, Gower St., London W. C., England.*
- OSTERUD, HJALMAR L., A.B., A.M., Teaching Fellow in Anatomy, *Institute of Anatomy, University of Minnesota, Minneapolis, Minn.*
- OTT, MARTIN D., A.B., Fellow in Anatomy, *University of Minnesota, Institute of Anatomy, Minneapolis, Minn.*
- REINKE, EDWIN, Ph.D., Associate Professor of Zoology, *Vanderbilt University, Nashville, Tenn.*
- ROBINSON, BYRON L., A.B., M.A., Teaching Fellow in Anatomy, *Institute of Anatomy, University of Minnesota, Minneapolis, Minn.*
- SANFORD, ELDON WILLIAMS, M.A., Ph.D., Assistant in Anatomy, *Johns Hopkins Medical School, Baltimore, Maryland.*
- SULLIVAN, WALTER EDWARD, A.M., Ph.D., Professor of Anatomy, *Tufts College Medical School, 416 Huntington Avenue, Boston, Mass.*
- WARREN, JAMES H., A.B., M.D., Assistant Professor of Anatomy, *College of Medicine, Ohio State University, 469 Indianola Bld., Columbus, Ohio.*
- WATSON, DAVID MEREDITH SEARS, M.Sc., F.Z.S., Lecturer in Vertebrate Paleontology, *University College, Gower St., London W. C., England.*

On motion, the Secretary was instructed to cast a ballot for all the candidates proposed by the Executive Committee. Carried.

The Secretary announced the following names as having been dropped from the list of members on account of non-payment of the last two years' dues: Dr. J. H. Hathaway, Professor of Anatomy, Detroit Medical College; Dr E A. Spitzka, 63 East 91st St., New York; and Dr. P. A. West, Johns Hopkins Medical School, Baltimore, Md.

It was announced by the Secretary that the following committee had been appointed during the past year to represent the Science of Anatomy in the National Research Council: Chairman, H. H. Donaldson; members, F. L. Barker, R. R. Bensley, Irving Hardesty, Aleš Hrdlička, G. C. Huber, C. M. Jackson, F. P. Mall (deceased) and C. R. Stockard.

Announcement was also made of the action of the Executive Committee to set aside a sum up to the amount of \$40 to be used by the Committee appointed at the last annual meeting to consider the nomenclature relating to the Sympathetic Nervous System.

Professor Huber made a report of progress for the above committee, and the committee consisting of Professors Huber, Hardesty and Ranson was continued.

Professor Huber then moved that the association request The Wistar Institute to publish the abstracts of the papers presented at this meeting in the January number of *The Anatomical Record* as has been done in the past. The motion was seconded and carried.

Dr. Greenman, the Director of The Wistar Institute, expressed his willingness to continue to publish the abstracts if the Association considered this a desirable thing to do.

On motion the business session adjourned.

SATURDAY, DECEMBER 29. A SHORT BUSINESS SESSION FOLLOWED THE MORNING SCIENTIFIC SESSION.

It was moved by Professor Huntington and voted that the Association express through the Secretary its thanks and sincere appreciation of the cordial hospitality and the unparalleled manner with which the Association had been accommodated and entertained by the University of Minnesota. In particular the thanks and appreciation of the Association are expressed to Professors Jackson and Lee and their associates in the Institute of Anatomy.

The meeting was then adjourned.

CHARLES R. STOCKARD,

Secretary of the Thirty-Fourth Session of the American Association of Anatomists.

ABSTRACTS OF PAPERS
PRESENTED AT THE
THIRTY-FOURTH SESSION
OF
THE AMERICAN ASSOCIATION OF ANATOMISTS
DECEMBER 27, 28 AND 29, 1917
AT
MINNEAPOLIS

ABSTRACTS

1. *The behavior of the phagocytic cells of the peritoneal fluid toward particulate matter.* WILLIAM H. F. ADDISON and J. MONROE THORINGTON, University of Pennsylvania.

By comparing the behavior of peritoneal-fluid cells toward coarse suspensions with their reaction toward more finely divided matter, something is learned of the differences in range of activity of several phagocytic-cell types, and factors are suggested for consideration in the analysis of phagocytosis. The experimental animal was the albino rat and we have chiefly made use of carbon suspension, filtered carmine, and colloidal trypan blue.

After injection, a visible phagocytic reaction to carbon suspension appears within the non-granular macrophages in about two hours, the reaction advancing markedly in from four to six hours. On the other hand, filtered carmine appears at from eight to twelve hours, while colloidal trypan blue is not usually visible before 24 to 36 hours. An important factor in phagocytosis is the state of irritability of the cell membrane. Our interpretation is that we are dealing with relatively non-toxic systems, each producing visible phagocytosis with a rapidity dependent upon the degree of irritation which its particles exert upon the phagocytic cells. Thus, particles of large size produce phagocytosis more rapidly than smaller particles. In colloids, if the size of the molecular aggregate be increased, as by electrolytic precipitation, the rapidity of phagocytosis is accelerated. In none of our experiments were the basophilic or eosinophilic cells phagocytic. Phagocytosis is shown principally by the non-granular macrophages, and, in the case of carbon and carmine, by the polymorphonuclear leucocytes which appear secondarily and which exhibit a more limited range of phagocytic activity.

2. *On the development of the eyelids in the albino rat.* WILLIAM H. F. ADDISON and HAROLD W. HOW, University of Pennsylvania.

Two noticeable features are the late period in gestation at which the eyelids develop and the rapidity of their formation. At the end of 17 days' gestation, the lids are merely slight ridges, but by the end of the eighteenth day the eyelids have met and fused. This is but 3 days before the normal time of birth. Comparing this stage of development of the eyelid in rat with several other species, we find that in rabbit (*Lepus*), with gestation period of from 28 to 30 days, the eyelids fuse at 20 days. In pig (*Sus*), with a gestation period of about 120 days, the lids fuse between the thirty-fifth and fortieth days. (Estimated from tables by O. Charnock Bradley, *Jour. Anat. and Phys.*, 1906.) In man the lids fuse about the seventieth day. The opening of the lids in the rat usually takes place on the fourteenth day after birth, and in man about the end of the sixth fetal month.

A comparison of the histological structure of the retinae of rat and man at the stages 1) of fusion and 2) of opening of the eyelids

shows a marked similarity. In each, at the time of fusion of the lids, the cellular layer of the retina shows a subdivision into two zones. At time of opening of lids, all layers of the mature retina have been established. There is apparently correlation between the development of the eyelids and of the retina.

3. *The relation of normal thyroid-gland development to bodily growth and differentiation in Rana, Bufo, and Amblystoma.* BENNET M. ALLEN, University of Kansas.

In *Amblystoma* both fore and hind limbs begin to grow before any colloid is formed in the thyroid gland. In *Bufo* it appears almost immediately after limbs have begun to grow, while in *Rana pipiens* it appears practically simultaneously with anlage of the hind limbs.

In all three forms there is a rapid growth of the gland, and this corresponds closely with limb development. In all three forms the thyroid gland is well developed and contains a large amount of colloid long before metamorphosis is completed.

In axolotls of 140-160 mm. length from Colorado the thyroid gland was found to be approximately of equal size and structurally similar to that of adult *Amblystoma tigrinum*. Colloid was present in large amount in both, but the axolotls were not well enough preserved to enable one to judge of its density.

Although the thyroid gland of *Bufo* is actually smaller at metamorphosis than that of *Rana* or *Amblystoma*, its proportion to body size is greater than in either *Amblystoma* or *Rana*. This is probably correlated with the shortness of its larval life and the greater rapidity of its metamorphosis.

There is a clear correspondence between the normal development of the thyroid gland and normal progress toward metamorphosis, although limb development may be partly independent of it.

4. *Further studies upon amphibian larvae from which the anterior lobe of the hypophysis had been removed.* BENNET M. ALLEN, University of Kansas.

The anterior lobe of the hypophysis was removed from larvae of *Rana pipiens* and *Bufo lentiginosus* as described in an earlier paper. The observations previously published were verified and much extended because of greater success in rearing the operated tadpoles. Several are still alive.

Limb development in both species is greatly retarded, running parallel with the condition in tadpoles from which the thyroid gland has been extirpated.

In *Bufo* there is a color change to a light yellow-brown, and contrary to the case in *Rana* there is little retardation of bodily growth.

The pars nervosa of the hypophysis forms normally in tadpoles, both *Rana* and *Bufo*, from which the anlage of the anterior lobe has been removed. There is of course no pars intermedia formed.

Gonads of operated *Rana* tadpoles were compared with normal con-

trols of the same size killed several months before. They showed the same features as to size, structure, and germ-cell development as seen in the controls. The same correspondence in the gonads was noted when comparison was made with some small thyroidless tadpoles of the same size killed at the same time.

The retardation of bodily growth in *Rana* prevented the gonads from reaching the size attained in the controls at metamorphosis three months before. In *Bufo*, however, the operated tadpoles reached a bulk double that at metamorphosis. Correspondingly, the gonads and germ cells developed far beyond the condition attained at the time of metamorphosis in the controls.

5. *A method of fixing rat testis by which both cytological details and the normal relationship between interstitial tissue and the tubules are obtained.* EZRA ALLEN, Philadelphia School of Pedagogy.

The unfortunate separation of the interstitial tissue from the tubules in the rat testis as usually obtained may be obviated by injecting the blood-vessels with picro-formol-acetic-chromic acid-urea fixative ('B-15'), after washing out the blood by normal salt or Locke's solution. Fluids and animal are kept at about 38°C.

When the organs are seen to be quite hard they are removed, cut into plates from 2 to 4 mm. thick with a safety-razor blade, and placed in fresh warm fixing fluid for about an hour. Further treatment is as described by the author in his article on technique in *The Anatomical Record*, vol. 10, July, 1916.

The slight pressure needed can be obtained from the laboratory air supply or by means of an atomizer bulb. In either case, the source of pressure should act upon the air in an air flask, which in turn is connected with the bottle containing the injecting fluid. A mercury manometer attached to the air flask shows the amount of pressure used.

The method fixes all organs equally well. It preserves intact the delicate vessels in the central portion of the villi. In the testis I have obtained the chromosomes well separated and thoroughly workable in those stages in which sad clumping is the rule. The histological picture is perfect. Since the interstitial tissue is not torn loose from the tubules, its relative volume is easily measurable.

6. *Movements in the visual cells and retinal pigment to light of graded intensities.* LESLIE B. AREY, Northwestern University Medical School.

The visual cells and retinal pigment of many of the lower vertebrates exhibit striking movements in light and in darkness. Previously reported experimentation having established that the rapidity of these changes had been greatly overestimated, the validity of a similar widespread impression regarding their extremely low threshold of sensitivity was next investigated.

Such a determination is important in view of a further (but discord-

ant) assumption that the positional changes of the visual cells in bright light and dim light favor cone-vision and rod-vision respectively, while the corresponding movements in the retinal pigment also mechanically increase visual efficiency. In other words, to derive the reputed adaptive benefits from such photomechanical changes, the responses in dim light must be essentially identical with those known to occur in total darkness; this assumption, however, is wholly gratuitous.

The responses of these elements to light of graded intensities prove that the threshold of stimulation is surprisingly high. In general, the maximum light-response is first elicited at an intensity which just permits the reading of ordinary print. Hence the assumed high photic sensitivity of the visual cells and retinal pigment is disproved, while the mechanical conditions for a theoretically more efficient twilight-vision and bright light-vision are established on an experimental basis.

7. *The development of the pars tuberalis of the rabbit's hypophysis.*

WAYNE J. ATWELL, Department of Anatomy, Medical School, University of Michigan.

For the rabbit it has been possible to trace the development of the paired anlagen of the pars tuberalis of the hypophysis from an earlier stage than that given by Tilney ('13) for the chick and the cat, or by Miller ('16) for the pig. From the thickened epithelium which early lies in front of Rathke's pocket two thickened ridges are developed. These ridge-like eminences may be called the lateral lobes, and are evident in embryos of 10 days. At 14 days these lobes have begun to grow out laterally and are more sharply constricted from the body of the hypophysis.

The lateral lobes are the anlagen of the pars tuberalis of the adult hypophysis. They begin to be in relation with the brain wall at 16 days of development, and by 19 days a considerable portion lies spread out under the diencephalic floor. There are present at this stage two blunt nasal horns extending toward the optic chiasm and two sharper caudal horns extending backward to surround the neck of the neural lobe. The caudal horns have completely surrounded the infundibulum and have met in the mid-line by the end of the twenty-eighth day. The nasal horns fuse with each other a day or so later.

Since the lateral lobes of the mammalian hypophysis may be seen early in development, it is now easier to consider them homologous with the lateral lobes of the reptilian hypophysis.

Because of its paired origin, the anterior part of the pars tuberales cannot be homologized with the 'Vorraum' of the reptiles, as is done by Woerdeman ('14).

8. *Observations on the movements of chick embryos.* O. V. BATSON, Anatomical Department, University of Missouri. (Introduced by E. R. Clark.)

The spontaneous rhythmic movements of chick embryos, which occur periodically throughout the greater part of the incubation period, were found to begin at 84-96 hours in chicks incubated at 38°-39°. Contrary to previous findings, movements in chicks around 96 hours occurred as a response to stimulation with a needle, especially when applied over the myotomes in the wing-bud region. Later stages have not yet been tested.

Complete section of the cord in three-day chicks does not modify the movements, and chicks so operated upon show no physiological or gross anatomical differences from unoperated chicks after hatching.

After removal of a section of the cord in the lower cervical region for a distance of three body segments, at 96 hours, the usual rhythmic movements, involving the entire body, were still present at six days.

After incomplete removal of the cord posterior to the wing-bud, at three days, rhythmic movements were still observed at seven days.

It is clear, therefore, that the periodic rhythmic movement of chicks is probably not a neuro-muscular phenomenon:

Rhythmic periodic movements persist if the egg is incubated at reduced temperatures after movement has begun. Periodic motility is not lost until 20°C. is reached. Raising the temperature to 20.5°C. induces motility. Rhythm begins at 21°C. At no temperature is there a quiescence indicating a latent period of adaptability.

9. *Histological changes in the placenta in the Toxaemias of pregnancy.* J. L. BREMER, Harvard Medical School.

In 1915 I called attention to certain thin epithelial plates to be found in the surface layer of the placental villi, in intimate connection with the underlying fetal capillaries, similar in appearance and relations to the epithelial plates of the visceral layer of the capsule of the renal or mesonephric glomerulus, and showed that such plates were present in the placenta only during the degeneration or absence of the mesonephros in any particular type of embryo. It was suggested that the presence of these plates showed the ability of the placenta to remove from the fetal blood certain excretory substances and to assume for the fetus the function of the glomeruli. The function of the renal or mesonephric tubules may be assumed by portions of the syncytial surface layer of the villi.

Normally the plates are widely scattered and only found after careful search. In certain toxæmic or eclamptic placentae, on the other hand, they are very numerous in every microscopic field, so that the fetal blood in the greater part of its course through the placental capillaries is separated from the maternal blood only by a thin osmotic membrane, composed of fetal endothelium and epithelial plate. The fetal capillaries are often dilated, but this does not seem to be

the cause of the increased extent of plates, by simple stretching, since the thicker synchytial layer is at the same time reduced in extent.

10. *Early stages in the development of the femur of the pig with reference to the influence of muscular activity upon its ossification.* EBEN CAREY, Department of Anatomy, Creighton University, Omaha, Nebr.

The earliest bone formed about the middle of the cartilaginous femur has been shown previously (Anat. Rec., vol. 11, no. 6) to develop more rapidly on the aspect directed towards the quadriceps extensor muscle than on that which is directed toward the hamstring muscles. The present paper attempts to correlate this unequal growth with the combined muscle forces manifested in the rotation of the limb. The preaxial border of the limb begins to turn mesiad in embryos of 19 to 22 mm., and rotation is completed in embryos of 40 to 50 mm. With the inception of rotation the femur begins to acquire a curvature, the convexity of which is directed towards the quadriceps extensor muscle. That the thigh musculature is capable of contracting at this period is shown by its response to Faradism in the living embryo. In the development of myofibrils the quadriceps extensor muscle is appreciably in advance of the hamstrings. The curvature of the femur, therefore, coincides with the rotation of the limb and the manifestations of contractility on the part of the thigh musculature.

A fibroblastic perichondrium appears first on the weakest aspect of the curved cartilage, viz., the convex surface at its region of maximum bending. The greater density of this tissue seems indirectly to favor senescent changes in the cartilage by preventing the access of blood-vessels. At all events, the use of injections reveals the presence of continuous vessels outside of the fibroblastic tissue only, while on the concavity, in the less modified mesenchyme, they approach nearer the cartilage. Bone appears first upon the convexity; and in subsequent stages develops there more rapidly than on the concavity. This early bone formation coincides in time with the manifestation of contractility of the thigh musculature and in site, like the antecedent fibrogenesis, with the region of greatest mechanical tensile stress incidental to the rotation of the limb and bending of the femur.

11. *The development of the lymphatics in the stomach of the embryo pig.* JAMES R. CASH, Anatomical Laboratory, Johns Hopkins University. (Introduced by R. S. Cunningham.)

By injecting the retroperitoneal sac in embryo pigs, it appears that, at about 30 mm., numerous lymphatic sprouts pass from its anterior part onto the stomach at the esophageal opening, around which they develop annularly. From this ring lymphatics grow in all directions, but especially along three paths, i.e., the lesser curvature, toward both cardia and pylorus, while from the caudal side of the ring two principal lymphatic vessels sweep ventralward, under the spleen, to the greater

curvature, along which they run toward both cardia and pylorus, anastomosing with the branches running to these points from the esophageal ring. The entire stomach is well covered with lymphatics at 60-70 mm., growth taking place in all directions from the ring and its principal branches. The retroperitoneal sac also sends several vessels directly to the pylorus through the duodenal mesentery. In the pyloric region, especially in the older specimens, 70-150 mm., the lymphatic plexus is seen to be much more dense and its vessels of smaller caliber than elsewhere in the stomach. Such facts may be of significance in relation to metastatic growths in this region.

Microscopically, two principal gastric, lymphatic plexuses are seen: one in the loose subserous tissue, the other in the submucosa. Both plexuses are very dense and their vessels relatively large. They are connected by a much less dense plexus traversing the muscularis. From the submucosal plexus numerous branches to the mucosa are seen which run in close relation to the blood-vessels.

12. *The effect of the heart-beat upon the development of the vascular system in the chick.* W. B. CHAPMAN, Anatomical Laboratory, University of Missouri. (Introduced by E. R. Clark.)

In order to test the question as to how much the development of the main vessels of chick embryos, particularly those of the yolk sac, is dependent upon mechanical factors concerned with the circulation, the heart was removed before circulation had been established, with the following results:

The embryo and area vasculosa remain alive for eight days after the operation, and considerable growth takes place, particularly in the area vasculosa.

The development of blood-vessels proceeds in a normal manner a short time beyond that at which the circulation usually commences. During this time there are formed in the extra-embryonic region vessels identical with the normal anterior vitelline veins, which fuse anterior to the embryo as in normal chicks, while the sinus terminalis passes through a cycle of development which markedly imitates the normal. On the other hand, certain vessels which normally differentiate early, the omphalo-mesenteric arteries and veins and the posterior vitelline veins, are not formed.

With the expansion of the vascular area, there is a continued formation of new capillaries; the property of sprout formation being apparently retained until death. After the third day, however, this is confined to the marginal portions of the area. Near the embryo, in the area pellucida, new formation has ceased at three days, and regressive changes commence; connecting capillaries are retracted, leaving isolated or nearly isolated endothelial blisters distended with fluid or cells. This regressive process advances gradually into the vessels of the area opaca.

13. *Phagocytosis of carbon and carmine granules in the transparent tails of tadpoles.* ELIOT R. CLARK and ELEANOR LINTON CLARK, Anatomical Laboratory, University of Missouri.

Small amounts of india ink and of suspensions of carmine granules were injected into the transparent tails of tadpoles and the region observed, on successive days, under the compound microscope, with the tadpoles anaesthetized with chloretone.

Leucocytes were the first cells to react to the presence of these foreign particles, migrating toward them and actively engulfing them. Some of these leucocytes, containing foreign granules, were observed to enter near-by blood-vessels. Others wandered off through the tissue spaces of the tail.

A day after injection, the stellate connective tissue cells began to ingest the foreign particles. Carbon and carmine granules thus phagocytized were located on the branched processes and in the cell bodies at the base of these processes. In such a transparent region, where individual living cells may be observed and followed for days and different cell types identified with ease, it is clear that mesenchyme cells are active phagocytes of foreign particles.

Lymphatic capillaries were not observed to grow toward the injected carbon or carmine; but when the granules were injected into the lumen of a lymphatic, the endothelial cells took up these foreign particles and stored them in the perinuclear areas.

14. *On the reaction of certain cells in the tadpole's tail toward vital dyes.* ELEANOR LINTON CLARK and ELIOT R. CLARK, Anatomical Laboratory, University of Missouri.

In the course of observations on the growth and reactive powers of the cells and tissues in the transparent tails of tadpoles, it seemed advisable to study the effect of vital staining on these cells.

Tadpoles were placed in solutions of various dyes and, after staining, were observed in a micro-aquarium, under chloretone anaesthesia. The three dyes, neutral red, bismark brown, and trypan blue, were used almost exclusively, because of the similarity of their action and because they all stained the lymphatic endothelium with especial distinctness.

The more highly diffusible of these dyes—neutral red and bismark brown—stain the cells more rapidly than the colloidal dye, trypan blue. Neutral red and bismark brown stain small, regular and apparently preformed granules in the epidermal cells. In addition, the contents of a richly branching subepidermal system are brilliantly stained with neutral red. Trypan blue does not stain the epidermis. All three dyes stain an occasional, probably preformed granule in the walls of blood-vessels. Neutral red, bismark brown, and trypan blue are all deposited as accumulations of dye granules in the perinuclear areas of the lymphatics, in certain wandering cells and leucocytes, and on the processes of the mesenchyme cells. The physiological relationship shown by this reaction toward these vital dyes on the part

of these different types of cells is probably due to their common property of phagocytosis.

15. *On the origin of the corpus luteum of the sow from both granulosa and theca interna.* GEORGE W. CORNER, Anatomical Laboratory, University of California.

The ovary of the sow possesses certain advantages for the solution of this problem. The paper is based upon a large series in which the stage of the reproductive cycle was determined by observation of the living animals and of their ova. The results may be summarized as follows:

In swine the membrana granulosa is retained intact after the rupture of the Graafian follicle. Its cells increase in size without division, their cytoplasm becomes laden with lipid substances, and they become the larger elements commonly called 'lutein cells' in the fully formed corpus luteum. The membrana granulosa is invaded by blood capillaries from the theca interna, which ramify to form an extensive vascular plexus throughout the new structure. The large lipid-laden cells of the theca interna are increased in number by mitotic division, lose many or all of their fatty inclusions, and pass into the corpus luteum to become lodged between the granulosa cells throughout the whole structure. There is no evidence that cells of the theca interna are ever converted into fibroblasts of the usual spindle-cell type or that they lay down the fibrils of the close-meshed reticulum which is present in the corpus luteum. There appears to be good evidence that some of the theca interna cells persist throughout pregnancy as distinct elements of the corpus luteum, but the exact fate of all of them cannot be learned by present methods because of a confusing resemblance between some of the theca and some of the granulosa derivatives.

16. *Observations on brachydactylism in the fowl.* C. H. DANFORTH, Department of Anatomy, Washington University of Medical School.

A form of brachydactylism affecting particularly the fourth digit is of common occurrence in the fowl. It is usually associated with booting (feathered tarsi). The extent to which the fourth toe is shortened ranges from a condition in which all five phalanges are present, but with a total length slightly less than normal, to a condition in which the toe is greatly shortened and the number of phalanges reduced to two. The fourth phalanx is the first to be affected, followed by the third, and then by the fifth. The skeletal elements seem to disappear through a process of coalescence rather than one of suppression.

Examination of developmental stages show that the brachydactyl digits are already noticeably shortened at a time when the cartilaginous anlagen of the phalanges are still in a rudimentary condition, which suggest that the brachydactylism is due not to a defect inherent in the skeletal system, but more probably to an influence that acts on the toe as a whole. The possibility of booting as a causative

factor seems to be definitely eliminated by the fact that brachydactylism may be clearly apparent before the first feather germs appear on the tarsi. It seems probable that both conditions are induced by some common cause, which is effective from the eighth to the tenth day of incubation.

Breeding records indicate that brachydactylism is transmitted in about the same proportions as polydactylism and booting. With the latter it shows a close correlation, with the former none.

17. *Further experiments with colloidal dyes.* HAL DOWNEY, University of Minnesota.

Sections of vena cava or portal vein tied off from $\frac{1}{2}$ to $2\frac{1}{2}$ hours after intravenous injection (the animal being kept alive in the meantime) of trypan blue or pyrrhol blue frequently contain numerous polymorphonuclears with dye granules. Similar cells may also be found in the spleen pulp, liver, and lung. They are more numerous if the vessels and organs are removed some time after the death of the animal.

Subcutaneous injections of these dyes result in the migration of numerous polymorphonuclears into the tissue in from 5 to 24 hours. They will rapidly gather up any free dye available and store it in the form of granules. If, however, all the dye is bound to cells and fibers of the connective tissue, when the polymorphonuclears reach the scene they will get none of it.

The granules of eosinophil leucocytes of rat stain brilliantly in trypan blue and the cells degenerate rapidly. In the early stages endothelial cells, fibroblasts, and lymphocytes also show the toxic effects of the dyes, but most of these cells are able to recover. Their nuclei enlarge and absorb much of the dye, and frequently some of the cytoplasm also. The latter may show diffuse staining. Later the dye is liberated from these cells and stored in the form of granules in lymphocytes, fibroblasts, and clasmatocytes.

Much of the dye is absorbed from the subcutaneous tissue by blood capillaries and larger vessels, and the polymorphonuclears within these vessels frequently contain dye granules.

18. *Studies on the ovary of the spermophile with special reference to the corpus luteum.* DELLA GAY DRIPS, Institute of Anatomy, University of Minnesota. (Introduced by Thomas G. Lee.)

The cycle of changes occurring annually in the ovaries of *Citellus* is presented with detailed histologic descriptions of the corpus luteum at each stage of its development. Specific stains are used to bring out the nuclear and protoplasmic characteristics of the luteal cells. Three phases are thus noted in the life cycle of the corpus luteum. First, is a phase characterized by the presence of great numbers of red granules, undoubtedly secretion granules in the protoplasm of the luteal cells. This phase embraces practically all of the period of pregnancy. Second, is the lipid phase, so-called because

of the abundance of lipid droplets in the protoplasm of the cells. This phase begins some time before parturition and lasts for about six weeks afterwards, which is also about the time that the normal involution of the uterus becomes complete. And, third, is the phase of regression. Certain experimental studies are reported, such as the effects of single and double ovariectomy on pregnant and non-pregnant animals. Single ovariectomy is negative in results. Double ovariectomy in non-pregnant animals causes a very gradual functional atrophy of the uterus. In pregnant animals, this procedure causes abortion, except when it is performed very late in pregnancy. From the results of the histologic and experimental studies it is concluded that the corpora lutea produce two internal secretions which preside over changes occurring in the uterus incident to pregnancy. The early secretion effects the normal implantation and development of the embryo and the late lipid secretion helps to bring about the normal involution of the uterus.

19. *The localization of hematogenic activity in the embryonic liver.* V. E. EMMEL, University of Illinois, Medical School.

The present paper is a presentation of the results of a study of phagocytic activity, giant cells and the differentiation of mesamoeoids and erythroblasts in the liver of pig embryos at different stages of development. The data is analyzed with reference to the growth of the liver and the correlated changes in hepatic structure.

20. *Feeding rats on glands of internal secretion.* J. F. GUDERNATSCH, Cornell University Medical College, New York City.

Seven sets of albino rats are being reared on a mixed diet. Six sets receive in addition desiccated thyroid, thymus, hypophysis, testicle, ovary, mammary gland, respectively. The following data can be given so far; they are *not* final, since the growth curves are changing constantly, due probably to an apparent increase in vitality of the entire stock.

The thyroid-treated animals form a group by themselves and cannot be discussed here.

The remaining rats may be put in three groups: 1) hypophysis, thymus; 2) normal; 3) testicle, ovary. The animals in (1) grow faster, especially hypophysis, than the normal; those in (3) slower. Testicle- and ovary-treated animals do not live as long as the others, decline in weight often begins under seven months. Males treated with ovary grow slightly better than those treated with testicle, while females treated with testicle grow somewhat faster than those fed on ovary.

Rats fed on hypophysis or thymus are fine breeders; the females build good nests and usually take good care of their young. Few young die early and seldom are entire litters lost during the nursing period. Rats fed on hypophysis seem to be somewhat precocious in their adolescence, and then sometimes the first litter is poor. Females treated with testicle or ovary are rather poor mothers often

some young die early or entire litters may be lost. Yet the average sizes of the litters are not very different. Indicating by ten the size of a normal litter, the other litters would range as follows: Ovary, 10.41; mammary, 10.33; thymus, 9.81; testicle, 9.75; hypophysis, 9.18.

In the thyroid-treated rats, if pregnancy sets in at all, there are many abortions or the young die early.

21. *Tests upon devices for the prevention of war deafness.* STACY R. GUILD, Anatomical Laboratory, University of Michigan.

Apparatus made to adapt devices to guinea-pigs. Injurious detonations produced by 0.45 Colt automatic, fired once at 15 cm. along 'protected' side. Killed after two days; injection fixation for cochleae; middle-ear parts observed during cochlear removal. Cochleae are still in process of preparation for sectioning; this report covers middle-ear observations only.

In numerous controls tympanic membranes ruptured regularly; and coagulate, usually associated with edema, was present. Of four animals with a "Scientific Ear Drum Protector 'Tommy,'" one had a single area of coagulate. Three animals with "Mallock-Armstrong Ear Defender," one had two areas of coagulate. Three animals with wax cone of Italian navy type; two had small amounts of coagulate. Four animals with vaseline-soaked cotton, one had radial streak of coagulate on the tympanic membrane and some along the tympanic ring and slight edema. Three animals with glycerin-soaked cotton, two had small amounts of coagulate with edema. Three animals with dry cotton, one had radial slit of tympanic membrane, all had coagulate, two with edema. Three animals with "Elliott Perfect Ear Protector," one had membrane off along $\frac{2}{3}$ circumference and was edematous, the other two had coagulate, one with slight edema. Three animals with a device invented by Dr. J. G. Wilson and Prof. A. Michelson, one had a 3-mm. hole in the membrane and all had coagulate.

Tests are being made by tambours as a check and will be reported at Minneapolis. The cochleae will give a further check on the relative efficiency.

22. *The development of the opossum during the first four days.* CARL HARTMAN, The Wistar Institute, Philadelphia, and the University of Texas. (Introduced by M. J. Greenman.)

Parturition occurs thirteen days after copulation and approximately ten days after ovulation. The first maturation takes place in the ovary; semination in the oviduct, where the albumen and the shell are added. Pronuclei were seen in uterine eggs. A variable amount of yolk is extruded at first cleavage. The process by which the first two pairs of blastomeres come to have the crossed arrangement will be discussed. The blastocyst is completed at about the 40-cell stage. Polar differentiation begins by attenuation of the non-formative cells, which are lineal descendants of one of the first two blastomeres. Cells in the thick formative area soon proliferate entoderm, which

process is completed about the end of the third day (egg, 0.8 mm.; vesicle, one-half that size). The albumen is gradually absorbed, and at about the end of the fourth day the mesoderm formation begins (vesicle, 1.6 mm. in diameter).

For the study of these stages preceding that of the primitive streak 84 uteri of 53 different females yielded 1055 eggs, of which about two-thirds were fertilized and normal. Photographs of the living eggs fresh from the animals (taken at Austin, Texas, by Dr. C. H. Heuser, of The Wistar Institute) as well as of fixed eggs and of preparations will be shown.

23. *The embryonic 'fissura hippocampi' in man.* MARION HINES, Department of Anatomy, University of Chicago and the Carnegie Institution of Washington, Laboratory of Embryology. (By invitation.)

Although the deep furrows, known as the transitory fissures of the medial wall of the cerebral hemisphere of fetal brains between the third and the fifth months are artefacts, the wall is not 'perfectly smooth' in embryos of seven to fourteen weeks. A shallow, but complete infolding of the wall extends from the rostral to the caudal pole. The nervous tissue, which lies at the bottom of this groove, consists of an inner, narrow, nucleated zone and a wide, cell-free area. Indeed, in the earlier stages, this is the only part of the cerebral hemisphere in which the matrix and the marginal velum of His are distinct. In a 11.6-mm. embryo, this area occupies the mediodorsal sector of the cerebral evagination. In one, 14 mm., it lies more medial, while in a 20-mm. it is almost centromedial. This sulcus, deepened by maceration, is doubtless the fissura hippocampi of amphibians and reptiles.

In the rostral part of the medial sector, ventral to the primordium hippocampi is an area, which resembles, in arrangement and position, the septal nucleus of lower vertebrates. The most dorsal part of this nucleus is continuous with the fascia dentata. A ventricular sulcus separates its ventral part from the primordium hippocampi and the definitive fascia dentata. The anterior commissure appears in the 39-mm. stage, the dorsal (pallial) commissure, in the 60-mm.

Therefore, in the course of its development, the medial olfactory cortex of man is as extensive as that of any other vertebrate.

24. *The reaction of selachii to vital stains.* E. R. and M. M. HOSKINS, New York University and Bellevue Hospital Medical College.

Intravenous injections into *Mustelus*, of the following substances, were made:

1. a) Trypan blue. Autopsy after five days. Phagocytosed freely by endothelium of larger blood-vessels within gills, hepatic sinusoids, and spleen, by parenchyma of liver, and by splenic cells. Many circulating phagocytes (probably endothelial cells and splenic cells) contained the stain. It was found also in the bile. The liver and spleen were dark blue in color. The stomach, spiral valve, kidney, digiti-

form gland, and skin were light blue in color from circulating stain. A very few particles of stain were found in the renal and digitiform-gland endothelium, and epithelium of the latter. b) Trypan blue, 36 hours. All organs light blue, but very little phagocytosis had occurred.

2. a) Carmine (coarse granules). Autopsies at various periods to four days. Results: Same as (1. a) in general, but cells are not able to ingest large granules easily. b) Filtered carmine. Not recovered.

3. Congo-red. Gross specimens, same results as above. Recovered in bile.

4. Neutral-red 1916. Results same as Congo-red. 1917, slight amount passed through the renal epithelium.

25. *On the anlage and morphogenesis of the chorda dorsalis in mammalia, in particular the guinea-pig (Cavia cobaya).* G. CARL HUBER, Department of Anatomy, University of Michigan.

In mammalia, the head process is a derivative of the ectoderm of the primitive node region in the axial portion of the embryonic area, and grows cephalad between ectoderm and entoderm to the region interpreted as the future pharyngeal membrane. The caudal end of the head process, through pseudo-growth and through rearrangement of cells, develops into the chordal canal, separated from both ectoderm and entoderm, with lumen which in the guinea-pig at no time reaches the dorsal surface of the ectoderm. With further development the chordal canal grows further and further cephalad, but at no time reaches the anterior limits of the head process. The chordal canal at all stages of development is in close relation with the underlying entoderm, which extends as an uninterrupted layer of plate-like cells ventral to the chordal canal. The chordal canal in further differentiation develops a cleft on its ventral surface, thus assuming the form of an inverted trough; the entoderm likewise develops a cleft, ventral to the open choreal canal, the entoderm extending, however, beneath the borders of the chordal plate, the latter at no time becoming definitely incorporated into the entoderm. Caudal to the primitive node, the entoderm is at no time interrupted ventral to the chordal anlage, and later, chorda dorsalis. It is the contention that the head process, and through this the chordal canal and plate and chorda dorsalis are to be interpreted as ectodermal derivatives.

26. *The innervation of the lateral-line organs in Squalus acanthias.* SALLY P. HUGHES, Grinnell College. (Introduced by H. W. Norris.)

The lateral-line nerve fibers in *Squalus acanthias* are distributed through: 1) ramus ophthalmicus superficialis VII to the supra-orbital canal and the suprarostal groups of ampullae of Lorenzini; 2) r. buccalis VII to the infraorbital canal and the ventral ampullae; 3) r. oticus VII to the lateral division of the infraorbital canal as far posteriorly as the supratemporal commissure, 4) r. mandibularis externus VII to the jugular ampullae and the mandibular and hyo-

mandibular canals; 5) r. supratemporalis IX supplying the first three ramuli to the main trunk canal; 6) r. supratemporalis X innervating the supratemporal commissure and sending six ramuli to the main canal; 7) r. dorsalis X with the next four ramuli to the main canal, and 8) truncus lateralis X to the main lateral canal of the trunk.

The innervation of the 'pit-organs', recently discovered by Johnston ('17), is through: 1) ramus supratemporalis X, to those anterior to the external opening of the endolymphatic duct; 2) r. dorsalis X, to the dorsal series; 3) r. mandibularis externus VII, to the mandibular series. The innervation of the group of pit-organs at the base of the yolk-stalk was not determined. There occur on each side two rudimentary lateral line organs: one on the anterior border of the spiracle, with innervation from the ramus oticus VII, strictly comparable in structure, position and innervation to the 'rudimentary canal-organ' found by Allis in *Amia*; and a second of similar structure, found near the mid-ventral line of the hyoid region, with innervation from the r. mandibularis externus VII.

This account agrees with Strong's abstract (1895), with Metcalf (1915), and with Landacre (1916). Johnston (1917) ignores the lateral line component in the IXth nerve and the branches of the r. supratemporalis X and r. dorsalis X to the main canal.

27. *Mutation in mammalian evolution.* GEO. S. HUNTINGTON, Columbia University.

In the phylogeny of the vertebrate lung the mammalian groups of the rodent Hystricomorphs and carnivore Mustelids show the derivation of the dominant asymmetrical type from an archeal plan in the following evolutionary series:

1. Primitive bilateral hyparterial symmetry with tracheal bulla, without cardiac bronchus: *Hystrix cristata*.

2. Bilateral hyparterial type with tracheal bulla and cardiac bronchus: *Taxidea americana*.

3. Bilateral hyparterial type with resolution of bulla into bifurcation of steni-bronchi: *Hystrix afro-australis*, *Hystrix longicauda*.

4. Establishment of prevalent asymmetrical mammalian type of right eparterial and left hyparterial bronchial tree as the normal condition: *Erethizon dorsatus*.

5. Within this genus the phylogenetic shift from the earlier to the subsequent condition is of relatively recent accomplishment, as evidenced by the occurrence of individual variants showing transitional stages.

6. In the Hystricomorph *Sphingurus* one of the early transitional stages, variant in *Erethizon*, appears as the fixed normal type.

7. The later transitional phase leading up to the final establishment of the prevalent mammalian tree appears as the normal type in the mustelid *Galictis*.

8. The evolutionary differentiation exhibited in this series is accomplished not by continuous variation or by migration of bronchial components, but by well-defined mutations.

It thus becomes possible to follow the relation of mutant variation to mammalian evolution in an organ, removed from direct environmental influences, within two closely limited mammalian groups.

28. *Additional notes concerning the development of the lobule of the pig's liver.* FRANKLIN P. JOHNSON, University of Missouri.

When the hepatic lobule reaches a certain maximum size, its central vein bifurcates; with its further increase in size, which usually takes place by a lengthening of the lobule at right angles to its central vein, the branches of the central vein grow toward the poles of the lobule. A splitting of the lobule follows shortly afterward, usually in the plane of original central vein and at right angles to its new branches. The splitting is accompanied in the later stages by an ingrowth of a new connective-tissue septum, which is later invaded by branches of the portal vein; in the younger stages by the branches of the portal veins alone. In this way, two lobules are formed from one, the old central vein later becoming a sublobular vein. The branches of the portal vein likewise bifurcate spreading themselves between the lobules. By repeated divisions whole groups of lobules arise from single ones, the genealogy of which may be roughly determined by a study of the branching of the hepatic vein. Occasionally new central veins arise from the hepatic and variations in the splitting process occur.

The increase in the size of the liver takes place by both peripheral and central growth, probably to a somewhat greater extent by the former. The latter process implies a rearrangement of the internal structures, but this takes place by a gradual displacement of large masses of liver tissue.

29. *On the question of commissural neurones in the autonomic ganglia.*

SYDNEY E. JOHNSON, Northwestern University Medical School.

The question of the origin of the spiral fibers and pericellular networks of autonomic ganglia has given rise to two opposed views. Ehrlich, Retzius, Langley, and others believe that they are terminations of cerebro-spinal, preganglionic neurones. Some authors (Dogiel, von Lenhossek, Huber) have, on the other hand, claimed that endings of other types of neurones (commissural, sensory) are also found in these ganglia. The writer has produced experimental evidence in favor of the first view.

Frogs were used for the experiments, as their autonomic ganglion cells are unipolar and the histological pictures are not confused by the presence of dendrites. Three different lots of frogs were operated.

Results of the first two lots of frogs were, if considered separately, inconclusive.

The third lot gave rather striking results. In these the spinal cord was destroyed and the trunci sympathici cut. This double operation eliminated the possibility (allowing time for degeneration) of preganglionic fibers reaching the posterior ganglia, while preganglionic fibers

could reach the anterior ganglia by running from the three anterior spinal nerves caudad or cephalad for some distance in the truncus sympathicus.

In the posterior ganglia all of the spirals and pericellular networks disappeared, while in the anterior ganglia a very few could still be demonstrated.

The evidence thus afforded appears to show: 1) that the spiral and pericellular fibers are of cerebrospinal origin; 2) that these preganglionic fibers may run some distance in the truncus sympathicus before terminating in a network on a postganglionic cell, and 3) that commissural connections do not occur in the autonomic ganglia of the frog.

30. The history of the nucleus caudatus and the stria terminalis in vertebrates. J. B. JOHNSTON, University of Minnesota.

The caudate nucleus consists of two parts, ventral and dorsal, which are distinct in structure and origin and in functional relations. The ventral portion is closely related to the olfactory and parolfactory nuclei, the bed of the anterior commissure and the medial part of the amygdaloid complex. The dorsal portion forms the chief part of the ridge which in man is called the 'tail' of the caudate nucleus. It is closely related to the lentiform nucleus, especially behind the internal capsule where these two enter into a common mass lateral to the amygdaloid complex.

The ventral portion is a part of the olfactory apparatus throughout the vertebrate series. The dorsal portion becomes prominent first in the reptiles where it forms the dorsal ventricular ridge. Its development in reptiles and mammals shows that it is derived from the lateral border of the pallium. The dorsal portion has fiber connections with the internal capsule and the pallium.

The stria terminalis is a complex bundle connecting the rostral and caudal parts of the olfactory apparatus. It and the gray mass in which it is imbedded (ventral portion of caudate) have been greatly elongated in mammals on account of the increased volume of the internal capsule.

31. The distribution of fractures of the femur. JOHN C. KOCH.

The mathematical analysis of the normal adult femur, presented by the writer at the last annual meeting of the association, is used as the basis of a comparison of the theoretical distribution of fractures of the femur and the actual distribution of the entire series of such fractures treated at the Johns Hopkins Hospital since its establishment in 1893.

The theoretical distribution is calculated and a graphic chart is constructed representing the relative tendency to fracture at any given segment, based upon the following assumptions:

1. The tendency for a fracture to occur at any point varies inversely as the least strength of the bone in that segment.

2. Blows of the same intensity are equally apt to be received at any point along the femur. Although blows may vary in intensity, they tend to be equally distributed.

3. The tendency to break at any point varies directly as the distance from the nearer support, the femur being supported at both ends in every case of fracture.

A second chart shows the percentage distribution of the fractures of the femur treated at Johns Hopkins Hospital, and every case in which it has been possible to determine with reasonable accuracy the position of the fracture has been included in the series studied, except those in which fracture was due to known bone disease and fractures of the head and neck of the femur.

A close agreement of the theoretical and actual distribution of the fractures of the femur is shown by the charts.

32. *The distribution of sympathetic neurones in the myenteric and submucous plexuses in the small intestine of the cat.* ALBERT KUNTZ, St. Louis University School of Medicine.

As determined by actual counts of the sympathetic cells present in transverse sections of the small intestine of the cat, sympathetic neurones are most numerous in the myenteric plexus at the pyloric end of the duodenum. Advancing distally, their number diminishes rapidly until a low point is reached in the upper ileum. Distal to this point, relatively little variation occurs until a point approximately 12 inches from the ileocolic valve is reached. From this point to the ileocolic valve there occurs a gradual and steady increase.

In the submucous plexus sympathetic neurones are most numerous approximately 2 inches distal to the pylorus. Advancing distally, their number diminishes rapidly until a low point is reached somewhat proximal to the low point in the myenteric plexus in the upper ileum. Distal to this point, there is a rapid increase until a relative high point is reached just distal to the low point in the myenteric plexus. Advancing farther distally, the number of sympathetic neurones diminishes very rapidly until another low point is reached, after which there occurs relatively little variation until a point approximately 12 inches from the ileocolic valve is reached. Distal to this point, there occurs a very rapid rise, reaching its maximum approximately 6 inches from the termination of the small intestine, then a sharp decline toward the ileocolic valve.

33. *The origin of cartilage from ectoderm in the urodeles.* F. L. LAND-ACRE and J. H. WARREN, The Ohio State University.

A study of urodele embryos demonstrates conclusively that the origin of all the branchial cartilages, except the second basi-branchial, and of the anterior portion of the trabeculae arise from the neural crest.

The neural crest migrates ventrally into the mandibular and branchial bars. The dorsal region of the neural crest forms portions of the V, VII, IX, and X ganglia, while the ventral portions differentiate into cartilages of the corresponding bars. The histological distinctions between mesenchyme derived from ectoderm and that derived from endo-

derm disappear in later stages, but during the earlier stages of growth are easily recognizable. These histological distinctions rest upon: a) The size of the cells; b) the size and number of yolk granules in the individual cells; c) the reaction to stains; d) pigmentation; e) the continuity of cell masses.

The greatest difficulties encountered in distinguishing ectodermal from endodermal mesenchyme arise where the two types of tissue overlap and mingle or where ectodermal mesenchyme is withdrawing from an area by migration and is being replaced by endodermal mesenchyme or where it is apparently undergoing cytolysis.

The distinction between ectodermal and endodermal mesenchyme indicated above seems possible at present only in types where there are yolk-laden cells, although it has been affirmed for other types. This distinction is recognizable in frog embryos, and if it exists in higher forms, it would explain some of the anomalies found in tumor formation in mammals.

34. *The implantation of the blastocyst and the formation of the decidual cavity in Dipodemyx.* THOMAS G. LEE, Institute of Anatomy, University of Minnesota.

This rodent, of the family Heteromyidae, is the third example thus far known among the Rodentia to be characterized by a perforation of the uterine epithelium and the passage of the ovum out into the stroma of the uterine mucosa to form an independent decidual cavity. The first, was the guinea-pig described by Graf Spee, the second was *Geomys*, previously noted by the present writer.

The perforation is through the antimesometrial wall, the blastocyst at the time of extrusion is larger and older than in the guinea-pig, the inner cell mass is distinct, the yolk sac large and differentiated into the inner visceral layer and the thinner parietal layer which is closely applied to enveloping trophoblast. The stroma of the mucosa becomes oedematous and filled with proliferating vessels; there is for a time a functional yolk-sac placenta.

There is entpy or the so-called inversion of germ layers, the inner cell mass elongates, becomes hollowed out to form the amnion, the ectoplacental conus is small.

In the uterine lumen at a point a short distance on either side of the site of perforation, a diverticulum is formed, which extends dorso-ventrally and laterally; by this means that area of uterine mucosa destined to form the walls of the decidual cavity is isolated except at the mesometrial pole to provide for vascular and nerve supply, and a septum at the antimesometrial pole; this extensive diverticulum is lined with the uterine epithelium.

35. *Bone-repair in the rat vitally stained with trypan blue.* C. C. MACKLIN, Department of Anatomy, Johns Hopkins University.

Healing fractures of the tibia, femur, and rib and healing trephine wounds of the skull were studied in twenty rats, the series extending

from the second to the seventy-first day of repair. Trypan blue, in 1 per cent aqueous solution, was administered intraperitoneally two days before death.

In the early stages the usual inflammatory reaction occurs. Macrophages in great numbers congregate at the site of the injury and phagocytize the tissue waste. They are probably derived principally from the small lymphocyte-like cells of the blood, but also from the local macrophages. Their period of greatest efficiency is from the third to the sixth day, inclusive. Most of them perish in situ, when their work is done, by undergoing disintegration.

A few polymorphonuclear leucocytes were associated with the macrophages. No dye granules were found in them.

During the period of removal of the provisional callus the numerous reticulum cells of its spaces develop intense phagocytic ability, manifested in their striking vital staining. They are regarded as being concerned in callus erosion to the extent that they phagocytize the products of callus breakdown—probably the tissue waste from the dissolving matrix. Their period of greatest efficiency is from the tenth to the twentieth day. They resemble in structure and function the macrophages of developing bone described by Shipley and Macklin (Amer. Jour. of Physiol., 42, p. 117).

Multinucleate cells, looking like osteoclasts, were found in the callus. Their number bore no direct relationship to the amount of callus destruction evidently progressing and they contained no dyestuff.

36. *On the behavior of Bufo and Rana towards colloidal dyes of the acid-azo group.* C. F. W. McCLURE, Princeton University.

Among the 140 larvae of *Bufo* placed on the third and fourth days after fertilization in solutions of Niagara and trypan blue (1:1500), 66 sectioned at intervals before the ninth day showed, with three exceptions, that no dye granules had been stored in any cell. In all except two of 31 larvae killed on the ninth day, and in 43 killed later, dye granules were invariably found. When larvae were placed in solutions after the ninth day, the ingestion and storage of dye granules by the cytoplasm of certain cells was essentially a question of hours.

Dye granules were observed in *Bufo* on the ninth day after fertilization in epithelium of pronephros and pharynx, Kupffer's cells, lymphatic endothelium, endothelium of renal-portal, postcardinal, and portal veins, in a few lymphocytes, and occasionally in the endothelium of aortic arches and inferior and external jugular veins. On tenth day dye granules were first observed in the mesonephric epithelium, and at a still later stage in the spleen. As Wislocki states, venous endothelium in *Rana* does not 'stain.' These and other experiments indicate that the initiation of phagocytosis in young amphibian larvae, is not influenced primarily by the length of time larvae remain in dye solutions, but is correlated with the attainment of a distinctive ontogenetic stage.

Partial immersion of body of larva or adult in solutions shows integument to be a portal of entry for the dye. Feeding experiments on adults show that dye may also reach circulation through alimentary canal.

Wislocki's method of vitally staining lymphatics does not specifically differentiate lymphatic endothelium and, like the injection method, is capable of demonstrating them only after continuous vessels are formed.

37. *The form of tracheal and bronchial cartilages.* (Lantern.) W. S. MILLER, Anatomical Laboratory, University of Wisconsin.

Horner, of Philadelphia, in 1839 gave the earliest description of the form of the cartilages at the place where bronchi divide, ascribing to them a saddle shape. Jonas King, of Guy's Hospital, followed in 1840 with a short paper which was illustrated by a few unsatisfactory drawings of cartilages in situ. King found that not all cartilages situated at the dividing point of bronchi had the characteristic shape ascribed to them by Horner. Since the time of King no attempt has been made to illustrate in plastic form the cartilages of the trachea or bronchi. The cartilages of the bronchi are usually described as being irregular plates scattered along the bronchi, gradually diminishing in number and size. Finding the usual descriptions unsatisfactory, reconstructions were made from the lung of man and various mammals to determine the actual shape and arrangement of the cartilages.

38. *On certain persistent units of anatomical structure.* ROY L. MOODIE, Department of Anatomy, College of Medicine, University of Illinois, Chicago.

The units of structure to which attention is called are those histological structures and impressions of soft parts which have been preserved in the rocks of past ages with sufficient clearness as to details of organization to give us adequate information as a basis for an opinion. Those persistent units of anatomical structure which will concern us here are: the osseous lacunae, the Haversian system of osseous lamellae, the perforating fibers of Sharpey, the cross striation of muscle fibers, the form of the brain, the form of the alimentary canal, the arrangement of the lateral-line organs, the sinus paranasales, and other matters of organization on which we have paleontological information.

The first osseous material to be developed on the bodies of the early vertebrates was in the form of a bony sheath, capping and partially surrounding the dorsal spine of the early shark-like vertebrates of the Ordovician and Silurian. These sheaths in microscopic section show typical osseous lacunae which do not differ in any essential respect from modern lacunae, save perhaps in the slighter development of the canaliculi.

The oldest known Haversian system, apparently, occurs in the

Devonian Arthrodire, Dinichthys. This is a primitive system differing only in minor respect from the modern Haversian systems of mammalian bones. The fundamental plan was laid down early, and no departure has since been made.

The oldest known perforating fibers of Sharpey are found in the humerus of a mosasaur from the Cretaceous of Kansas. These occur in bundles, very like modern fibers. In the material so far studied there is no evidence that these fibers penetrate a series of Haversian lamellae.

The cross striation of musculature was first made known by Dean. There is little difference in the striation of the Devonian shark, *Cladodolache*, described by Dean, and the modern shark. The ancient tissue presents coarser striations, but the plan is essentially the same.

The form of such structures as the brain in fishes, the alimentary canal in amphibians, the lateral-line canals in amphibians, and the sinus paranasales in early mammals all tend to show that there are certain features in anatomical structure which have been only slightly affected in the great evolutionary changes which have been brought about in other features of animal organization.

39. Studies on the Mammary Gland. IV. The histology of the mammary gland in the male and female albino rat from birth to ten weeks of age. J. A. MYERS, Institute of Anatomy, University of Minnesota, Minneapolis.

At the time of birth the attached end of the primary duct is represented by a solid cord of cells which attaches to the epidermis in the male and the medial side of the developing nipple in the female. The free end of the primary duct possesses an incomplete lumen. The secondary and tertiary ducts present walls of three or four cells in thickness. The cells nearest the lumina have not yet become arranged in definite layers. The walls of the terminal ducts are somewhat thinner than those just described. In rats of ten days the epithelium of all ducts from the primary through the terminal ducts is arranged in two layers. The inner layer is composed of cuboidal cells quite uniform in size, while in the outer layer the cells are more irregular in size and shape. At nine weeks the epithelium is still present as two layers in most of the ducts. In a few instances, however, the terminal ends present a single layer of cells.

Weigert's resorcin-fuchsin stain reveals a few elastic tissue fibers in the later stages, more having been observed in the first few weeks of life.

Glands of several early stages have been stained with Bell's differential fat stain, scarlet red, osmic acid, and Herkheimer's stain. At present no definite newborn secretion has been observed. In a few cases, however, small droplets of fat have appeared in the walls of the milk ducts.

40. *The eyeball and associated structures in the coecilians.* H. W. NORRIS, Grinnell College.

In the coecilians the typical amphibian eyeball musculature and eye-muscle nerves have been modified, first, by the degeneration of muscles and nerves to the point even of complete disappearance; second, by the transfer in function and anatomical relations of certain muscles from the eyeball to adjacent organs, as the retractor bulbi transformed into a retractor tentaculi, the rectus internus changed into a retractor of the tentacular sheath, the levator bulbi modified to a compressor muscle of the orbital glands. Genera studied: *Coeilia*, *Dermophis*, *Geotrypetes*, *Herpele*, *Ichthyophis*.

41. *Lateral asymmetry in chick embryos developing without circulation.* (Lantern.) C. W. M. POYNTER, University of Nebraska, Omaha.

In a series of chick embryos, in which the development was disturbed in order to study the process of disassociation, it was noticed that lateral asymmetry frequently occurred. The eyes which were among the first structures to show a reaction to the disturbance presented some interesting examples of disassociation and delayed development. These conditions possibly throw some light on one way, at least, in which *monophthalmica asymmetrica* may develop.

Embryos in which the circulation was destroyed or its development prevented by operation, showed 80 per cent in which lateral asymmetrical development or degeneration occurred; of these 100 per cent exhibited a greater reaction in the left eye.

Embryos placed in the refrigerator at 12 degrees for varying periods, then allowed to continue development, showed a large percentage of eye and ear deformities, but only a small number of examples of lateral asymmetry.

Embryos inoculated with *staphylococcus* showed 25 per cent asymmetry, only slightly over half of these being on the left side.

The lateral disturbance is not confined to the eyes, the ears presenting the same type of asymmetry, though less frequently, and the entire lateral half of the body may share in the delayed development or disassociation.

In this study the disturbances to development are so profound that in a short time death of the entire embryo occurs; consequently, there is no opportunity to observe a regenerative process.

These experiments suggest that the eyes are not equally resistant to all the factors operating; the left eye is more susceptible than the right, regardless of whether rotation occurs normally or is reversed.

42. *Afferent fibers of the truncus sympathicus and splanchnic nerves in the cat.* S. W. RANSON, Northwestern University Medical School.

The truncus sympathicus in the neck contains no sensory fibers, and in the upper thoracic segments only a few. But in the lower thoracic region, it contains a great many such fibers destined for the splanchnic nerves. These sensory fibers include myelinated axons of all sizes and

many that are unmyelinated. They come from the spinal ganglia by way of the white rami.

The splanchnic nerves are composed exclusively or almost exclusively of fibers derived from the white rami and contain in addition to the myelinated and unmyelinated sensory fibers also myelinated preganglionic efferent fibers. They contain few if any fibers arising from the ganglia of the truncus sympathicus.

The descending fibers from the white rami run in well-defined bundles in the truncus sympathicus, the afferent and efferent fibers from a given ramus mixed together, but separate from the fibers coming from the other rami. These bundles degenerate after section of the corresponding spinal nerve. If the roots of a spinal nerve are cut proximal to the spinal ganglion, the fine myelinated efferent fibers of the bundle degenerate and the sensory fibers stand out alone. If the roots are cut distal to the spinal ganglion, all the fibers of the bundle, including the unmyelinated sensory fibers, degenerate. The fibers from adjacent bundles intermingle very little if at all.

43. *Cyclic changes in the interstitial cells of the ovary in the woodchuck (Marmota monax).* A. T. RASMUSSEN, Institute of Anatomy, University of Minnesota.

From an examination of 144 ovaries, representing every month, it is evident that the interstitial cells vary greatly with the seasons of the year. They are minimal in late summer. During autumn and winter (involving hibernation) there is a slight gradual increase in the lipoids and hence in the size of the cells. There is no sudden change at the onset of hibernation but after waking up from winter-sleep (in March) and rutting begins, there is a marked hypertrophy. The cells increase in size and possibly in number. A few are almost free from large lipoid granules and the rest contain abundant cytoplasm between the fatty droplets. There is a distinct increase in fuchsinophilgranules. Maximum development is seen at the beginning of pregnancy.

With the growth of corpora lutea, interstitial cells decrease, but are particularly rich in lipoids.

In mid-summer, about two months after parturition, when corpora lutea are rapidly degenerating, the interstitial cells lose all or nearly all their fatty content. The nuclei generally decrease in size and but little cytoplasm remains. Possibly some cells disappear entirely. Mitochondria, which are mostly round with only a few short straight or slightly curved rods and which are demonstrable at all times, largely persist.

Thus the interstitial cells of the ovary closely parallel the changes in the homologous cells of the testis of this species. Pigment granules similar to those in the testis are not found in the interstitial cells of the ovary.

44. *On the growth of the various organs of the body during fetal life.* RICHARD E. SCAMMON, Institute of Anatomy, University of Minnesota.

A summary of a statistical study of the growth of the principal organs of the body during fetal life and of their average weights and normal variations in weight at birth.

45. *On the development and finer structure of the sucking-pad (Corpus adiposum buccae).* RICHARD E. SCAMMON, Institute of Anatomy, University of Minnesota.

A description of the general development of the sucking-pad during fetal life with a description of its structure at birth.

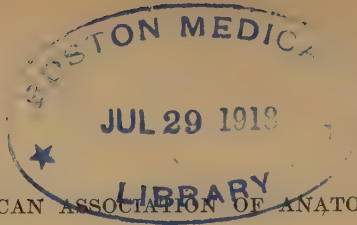
46. *On the time of obliteration of the fetal blood-passages after birth.* R. E. SCAMMON and E. H. NORRIS, Institute of Anatomy, University of Minnesota.

A statistical study of the time of obliteration of the lumina of the ductus arteriosus and ductus venosus and of the closure of the foramen ovale in man.

47. *Material for a study of the Megapodiidæ.* R. W. SHUFELDT, Washington, D. C.

This very elaborate memoir on the mound birds was completed two years or more ago, and accepted in Germany for publication in the Zoologische Jahrbücher. That MS. and its plates were last heard from in Jena, since which time the world war has come about. Since this, too, the entire manuscript, with its twenty-one plates containing many figures, some of which are colored, has been reproduced for publication, and is now ready to go to press. All the material upon which the work is based belongs in the collections of the Division of Birds of the U. S. National Museum; it consists of the skins and eggs of quite a number of the Megapodiidæ, including the skeletons of the Nicobar species as well as the rare Megacephalum maleo. A detailed account of the osteology of these latter two is presented. There are among the plates colored heads of Megapodius nicobariensis, M. cumingi, Catheturus lathamii, and Megacephalum maleo. The latter species is here figured for the first time, with the correct coloring for its head. All previous authors have represented this as being black; but, as recently pointed out by Renshaw, the casque is bright blue, the culmen red, and most of the bill pea green. This is a remarkably handsome bird in life, the plumage of its body being of a blackish brown, with green reflections on the tail. The most striking part of all its plumage, however, is the elegant pinkish salmon color of the entire under parts.

The close comparative study of all this goes to show that there can now be no question as to the Megapodes being a separate family from the Cracidæ, and most assuredly from other families of gallinaceous birds, as the guinea-fowls and turkeys. It is clear from what is set forth in the memoir, presenting, as it does, many new facts in the



morphology of the Megapodiidæ, and other matters related to them, that it does not tend in any way to disturb the views set forth by many previous writers with respect to their taxonomy. Indeed, it confirms a fact long ago announced by me, that is, what I pointed out as early as 1904 in the American Naturalist to the effect that the mound birds (Megapodiidæ) belong in the suborder Gallinæ (Family I.) next above the Cracidæ in a linear arrangement; and should the monograph from which these brief notes are abstracted settle this point, or even assist in settling it for all time, I shall certainly feel that my labor upon it has not been entirely devoid of useful results.

48. *The skeleton in the 'Kea parrot' of New Zealand (Nestor notabilis).*

R. W. SHUFELDT, Washington, D. C.

This paper presents a complete account of the skeleton of this remarkable bird, and is illustrated by sixteen figures on seven plates. No part of this work has ever appeared before and no full account of the 'Kea' has heretofore been published.

During the summer of 1917, the Department of Tourist and Health Resorts, New Zealand Government, presented to the National Zoological Park, at Washington, D. C., nine adult specimens of this famous 'Kea parrot' (*Nestor notabilis*). When the shipment arrived at the park, August 31, 1917, one bird was found dead in the crate and was transferred to the National Museum to be prepared as a skeletal accession to the collection. It is the description of this skeleton which forms the subject matter of the present paper. It has for its object the shedding of additional light upon what has already been set forth in literature by previous authors on the taxonomy of the genus *Nestor* or the place of that genus in the system. By avian systematists this has generally been held to be that, as a group, small as it is, it forms a separate family, namely the Nestoridæ. The late very eminent British ornithologist, Alfred Newton, F.R.S., sets forth in his Dictionary of Birds that "The position of the genus *Nestor* in the Order *Psittaci* must be regarded as uncertain."

Count T. Salvadori, in the Catalogue of Birds of the British Museum, after a very cursory examination of its skeleton, relegated these parrots to a family, Nestoridæ; many other writers have followed him in this regard.

Dr. Frank E. Beddard, F.R.S., in his excellent work on "The Structure and Classification of Birds" (London, 1898), devotes some little attention to *Nestor*. After passing in review what has been thus far worked out upon its anatomy, Doctor Beddard presents the suborder *Psittaci* as arrayed by Garrod in his work, and in it we find two families, one of which is the *Psittacidæ*. In this family the subfamily *Arinæ* is created to contain *Ara*, *Conurus*, *Bolborhynchus*, *Caica*, *Psittacus*, *Poeocephalus*, and *Nestor*. In other words, the 'Kea' in this classification is only entitled to generic rank, and belongs in the family *Psittacidæ*. Like so much of Garrod's work in the classification of birds, this is a totally unnatural scheme, as anyone

who has studied the skeletons of Conurus, Ara, and Nestor and compared them will contend. He almost invariably based his conclusions upon altogether too few characters.

The skull of Nestor, for example, presents many characters quite different from those of Conurus and the macaws, and this applies to other parts of its skeleton.

All this will be duly and most fully set forth in the memoir when published, of which this is but a very brief abstract.

49. *Weights of various parts of the brain in normal and underfed albino rats at different ages.* C. A. STEWART, Institute of Anatomy, University of Minnesota, Minneapolis.

The olfactory bulbs increase from an average of slightly more than 2 per cent of the normal brain weight at birth to more than 4 per cent at ten weeks. In the adult the relative weight (and possibly the absolute weight) apparently decreases.

The telencephalon and diencephalon (excluding olfactory bulbs) collectively form about 66 per cent of the entire normal brain weight at birth, 69 per cent at three weeks, and 63 per cent in the adult.

The crura cerebri, pons, and medulla oblongata collectively decrease from an average of nearly 27 per cent of the normal brain at birth to about 20 per cent in the adult.

The cerebellum increases from an average of 3.5 per cent of the brain in the newborn to approximately 14 per cent at ten weeks of age and later.

In underfed rats weighing 10 grams when three weeks of age the brain is considerably heavier than in normal younger rats of the same body weight, the increase being shared by each of the various parts of the brain mentioned above. The relative weights of the telencephalon and diencephalon (excluding the olfactory bulbs) and also of the brain stem (including crura cerebri, pons, and medulla oblongata) apparently decrease slightly in the test rats, while the cerebellum increases in percentage of the entire brain weight. The relative weight of the olfactory bulbs remains practically unchanged.

50. *Normal and abnormal development in individuals exhibiting different degrees of twinning.* (Lantern.) CHARLES R. STOCKARD, Cornell University Medical College, New York City.

A group of 38 individuals, ranging from a double-headed to a complete twin condition, was selected at random in a trout hatchery and given to me for study. These specimens have been arranged in a graded series and studied in order to determine the degree of perfection in the development of their heads.

The great majority of them, 26, are bilaterally symmetrical, the two heads being equal in size. Without exception, in all these cases the two heads are normal in general appearance, and so far as their eyes and mouths are concerned are typically perfect. Eleven of the young fish are asymmetrical; one head in the double-headed types or one

member of the joined twins being normal in size and perfectly developed, while the other head or body is inferior in size and in every case is abnormally developed, particularly in respect to its eyes.

Only one specimen of the 38 had both heads deformed, yet on analysis this one is in perfect accord with the group.

The conditions shown by these specimens furnish most valuable material for an understanding of the causes of many kinds of abnormal development, and they will be discussed from this standpoint.

51. Observations on gray hair and alleged sudden blanching of hair.

R. M. STRONG, Vanderbilt University Medical School.

Various statements occur in the literature of hair color, concerning the causes of grayness or canities. Usually it is recognized that absence of pigment is a cause, but it is also commonly stated that the entrance of air into hair is a factor. My own observations have led me to doubt whether gray hairs ordinarily contain any more air or other gaseous material than colored hair. All hairs have a great number of both internal and superficial reflecting surfaces due to incomplete fusion of the constituent cells, which alone can account for whiteness when pigment is not present to absorb the incident light.

Various standard text-books of dermatology still credit the old accounts of sudden loss of hair color. This subject has interested me for about fifteen years, and I have discussed it often with clinicians, especially dermatologists. Only one alleged case has come to my attention during this period. Hair specimens of this were obtained and the circumstances investigated carefully. No good evidence was obtained that the white hairs were blanched suddenly or were in any way abnormal. All statements in the literature of such phenomena were made in a less critical period than the present. It is my judgment that, until more satisfying evidence is obtained of the actual occurrence of such phenomena, we should regard sudden blanching of the hair as improbable. No method by which it could take place is known to me.

This is a preliminary report of work on gray hair, not yet complete.

DEMONSTRATIONS

1. *Experiments upon the glands of internal secretion in Rana and Bufo larvae.* BENNET M. ALLEN, University of Kansas.
2. *Positional changes in the visual cells and retinal pigment to graded intensities of light.* L. B. AREY, Northwestern University Medical School.
3. *Models illustrating the development of the hypophysis cerebri of the frog.* WAYNE J. ATWELL, Department of Anatomy, Medical School of the University of Michigan.
4. *X-ray plates illustrating anatomy in the living.* C. R. BARDEEN, University of Wisconsin.
5. *Models and corrosion preparations showing the branching of the hepatic ducts in human embryos and newborn.* E. A. BAUMGARTNER, Department of Anatomy, Washington University Medical School.

The hepatic anlage in a 4.2 mm. human embryo is round, extending cranially and ventrally from its wide connection with the gut. Hepatic trabeculae grow from its lateral and ventral surfaces. A short caudal portion bears no trabeculae and is probably the pars cystica. A single ventral pancreatic anlage projects from the right side of the caudal end of the hepatic outgrowth caudal to the pars cystica.

In a 7.5 mm. specimen the hepatic duct divides near its origin into a small right ductule and a very much enlarged plate-like duct from which hepatic trabeculae are given off in all directions. The gall bladder is attached to the common duct by a short cystic duct.

A model of a 17 mm. embryo shows the distal end of the gall bladder directed cranialward. The hepatic duct and its right subdivision are lengthened. Hepatic trabeculae arise from the right and left ducts. Another specimen of the same size shows several small hepatic ducts arising from the cystic duct, one of which anastomoses with a radicle arising from the hepatic duct. This specimen also shows an enlarged distal end of the hepatic duct, similar to that in younger stages.

Models of 25 mm. and 41 mm. embryos show growth in length of cystic and hepatic ducts. In the 41 mm. specimen the hepatic duct breaks up into several laterally-projecting ducts from which many hepatic trabeculae are given off.

Corrosion preparations of the hepatic tree in several new borns have been made. These show as a rule a right and a left hepatic duct with smaller and larger subdivisions spreading into the liver.

6. *Microscopical preparations of a closely graded series of hind limbs of pigs showing the early stages in the development of the femur and the thigh musculature.* EBEN J. CAREY, Department of Anatomy, Creighton University.

7. *Preparations illustrating the origin of the corpus luteum of the sow.* GEORGE W. CORNER, Anatomical Laboratory, University of California.

8. *Stages in the development of brachydactylism in the fowl.* C. H. DANFORTH, Department of Anatomy, Washington University Medical School.

Feet of brachydactyl chick embryos fixed on about the tenth day of incubation and stained *in toto* by the Van Wijhe method show various degrees of diminution in the cartilaginous skeleton of digits IV. The preparations are thought to indicate that the reduction in the number of phalangeal cartilages is due to a fusion of the anlagen of these elements. The skeletal elements of the feet of a few adult birds are shown for comparison.

9. *Material illustrating the early reactions of blood and tissue cells to colloidal dyes.* HAL DOWNEY, University of Minnesota.

10. *Microscopic sections of the ovaries of the spermophile (citellus) showing secretory granules and lipoids characteristic of the periods of the annual dioestrus cycle.* DELLA GAY DRIPS (Introduced by Thomas G. Lee), Institute of Anatomy, University of Minnesota.

11. *Demonstrations illustrating hematogenesis in the embryonic liver as correlated with different stage in hepatic development.* V. E. EMMEL, University of Illinois Medical School.

12. *Further observations concerning the relation of the aortic cell clusters and degenerating aortic rami.* The Demonstrations consist of a series of sections and drawings showing: (a) The Intimate Association of Aortic Cell Clusters and Arterial Cell Masses in Aortic Rami. (b) Aortic Cell Clusters in Relation to Atrophying Roots of the Superior Mesenteric Artery. (c) The Relation of Cell Clusters Within the Lumen of the Superior Mesenteric Artery to Degenerating Aortic Rami. V. E. EMMEL, University of Illinois Medical School.

13. *The growth of the limb-skeleton of Okapia Johnstoni.* F. W. HEAGEY, Department of Anatomy, Creighton University.

This material was collected by the Lang-Chapin expedition of the American Museum of Natural History in Belgian Congo, Africa. It has been loaned to the Department of Anatomy of Creighton University for study. This collection consists of six complete skeletons of Okapia ranging in size from an embryo 120 mm. in length to a young individual that has attained about one-third the adult growth.

14. *Further experiments with the effect of heat upon the chromosomes of Cumingia.* MARGARET M. HOSKINS, New York University and Bellevue Hospital Medical College.
15. *Specimens and slides of further experiments with thyroidectomy in Amphibia. (Rana Sylvatica.)* E. R. HOSKINS and M. M. HOSKINS, New York University and Bellevue Hospital Medical College.
16. *A wax model of the left half of the medulla oblongata of Squalus acanthias ("pup" stage), showing an analysis of the cranial ganglia.* SALLY P. HUGHES, Zoological Laboratory, Grinnell College.
17. *The effect of inanition upon the growth and structure of the supra-renal gland in the albino rat.* C. M. JACKSON, Institute of Anatomy, University of Minnesota.
18. *A wax-cast model of the human nasal cavity and paranasal sinuses.* C. M. JACKSON and C. E. CONNOR, Institute of Anatomy, University of Minnesota.
19. *An instrument for the measurement of human hairs.* A. E. JENKS, (by invitation), Department of Anthropology, University of Minnesota.
20. *Autonomic ganglia of the frog before and after degeneration of the preganglionic fibres.* S. E. JOHNSON, Northwestern University Medical School.
21. (a) *Neurological methods; celloidin sections; staining; mounting and storing sections.* (b) *Nucleus caudatus and other recent forebrain studies.* J. B. JOHNSTON, University of Minnesota.
22. *The implantation of the ovum and early development in the rodent dipodomys.* THOMAS G. LEE, Institute of Anatomy, University of Minnesota.
23. *X-ray photographs of injected blood vessels as illustrated by stereorentgenograms of the lung.* W. S. MILLER, University of Wisconsin.
By slight modification of Gage's corn starch injection mash using various pigments different degrees of density may be obtained.
24. *Certain persistent units of anatomical structure.* ROY L. MOODIE, University of Illinois.
25. *The arterial supply of the human hypophysis.* STUART MUDD, (introduced by Dr. R. J. Terry), Washington University Medical School, St. Louis.
Three methods are being used: a) Injection with thin celloidin and corrosion by artificial gastric juice—somewhat unsatisfactory be-

cause of difficulty of injecting finer vessels, and because relations of arteries to tissues are not preserved; b) wax reconstructions of thick colloidin sections of foetal specimens—sections not yet studied; c) dissection under binocular of gelatin—injecting vessels.

Brains for dissection are injected through the common carotid, with contra-lateral carotid, both vertebrals and external and internal jugular veins ligatured. Robin's Prussian blue and carmin have been used. The base of the brain in the region of the sella turcica and the underlying bone are removed and preserved in formalin. The brain and meninges are carefully freed from the underlying bone, dehydrated and cleared in cedar oil. They may then best be dissected under oil of wintergreen with a binocular.

The brains are dissected through their underlying meninges successively upon two planes: 1) an intradural plane, comprising the internal carotids and their branches within the cavernous sinus; 2) a subdural plane comprising the circle of Willis and its branches. Four brains only in the intradural plane have thus far been dissected.

In each of these four brains there are found, arising from each internal carotid at its first and superiorly convex flexure in the cavernous sinus, an artery of approximately one to two millimeters in diameter which quickly breaks up into several somewhat variable branches. These branches, together with an inconstant artery which may arise from the carotid in the sinus cavernosus more anteriorly, supply the semilunar ganglion, the third, fourth, fifth and sixth nerves in this region and the contiguous dura mater. One of the branches on each side, ramifying, courses between the layers of the dura across the posterior lobe; twigs are sent also to the dura and may even be sent to the anterior lobe.

The branch described is probably sufficient to supply the posterior lobe, but apparently does not form a considerable element in the supply of the highly vascular anterior lobe.

26. (a) *The fetal development of the mammary gland in male and female albino rats.* (Wax reconstructions and stained sections.) (b) *The development of the mammary gland in male and female albino rats from birth to ten weeks of age.* (Wax reconstruction, cleared preparation and stained sections.) J. A. MYERS, Institute of Anatomy, University of Minnesota.

27. *Preparations and drawings illustrating the structure of the truncus sympathicus rami communicantes and splanchnic nerves in the cat.* S. W. RANSON, Northwestern University Medical School.

28. *Histological preparations showing the cyclic changes in the interstitial cells of the testis and of the ovary in the woodchuck (Marmota monax).* A. T. RASMUSSEN, Institute of Anatomy, University of Minnesota.

29. *Monsters of excess and of defect.* DANIEL G. REVELL, Department of Anatomy, University of Alberta.

Photographs, roentgenograms and sections showing deduplications and deficiencies in chick, pig, human and other specimens.

30. *On the growth of the various organs of the body during fetal life.*

R. E. SCAMMON, Institute of Anatomy, University of Minnesota.

Field graphs and curves of the rate of growth of the various organs of the body during the greater part of fetal life, based upon material from autopsies in the Institute of Pathology of the University of Minnesota and on cases collected from the literature. Tables showing the average weight and the degree of variation in the weight of the principal organs of the body at birth.

31. *Sections showing the origin, development and finer structure of the sucking-pad in man.* R. E. SCAMMON, Institute of Anatomy, University of Minnesota.

32. *Various parts of the brain in normal and underfed albino rat at different ages.* C. A. STEWART, Institute of Anatomy, University of Minnesota.

33. *Van Wijhe preparations of the primordial cranium of the cat.* R. J. TERRY, Washington University Medical School.

Embryos measuring 10.5, 15, 24 and 30 mm. in length, prepared by Van Wijhe's method of staining and clearing, reveal in the clearest way the beginning, direction and extent of the processes of cartilage formation. Of special interest in these specimens is the evidence given of independence of chondrification of the otic capsule, parts in the cranial side wall and elements of the ethmoidal skeleton.

In the specimen of 10.5 mm. may be seen the hypophyseal cartilage, the beginning of the otic capsule, Meckel's cartilage, parachordal plate and lateral occipital arches.

The preparation of the 15 mm. embryo shows the septal, paratectal and paranasal cartilages, the ala orbitalis, ala temporalis, commissura orbito-parietalis, basal plate, hypoglossal foramen and lamina parietalis.

The cranium of the 24 mm. embryo is of special interest in giving evidence of the relations of the suprafacial commissure to the parietal plate.

Chondrification of the cranium has reached its maximum in the 30 mm. specimen.

34. *A teaching model of a 10 mm. pig embryo.* IVAN E. WALLIN, Marquette University.

35. *Models illustrating the early development of the liver and hepatic ducts in the mouse.* H. W. WELLMERLING, (introduced by E. A. Baumgartner), Washington University Medical School.

The liver in 3 mm. embryos is a wide outgrowth of the gut with many small projections. Ventral to the hepatic portion is the small, rounded anlage of the gall bladder, Hammar's pars cystica of the hepatic anlage.

The common duct in 3.5 mm. embryo has a wide dorsal connection with the gut and bears on its caudal surface the anlage of the ventral pancreas and a large gall bladder. Hepatic trabeculae are attached to the cranial surface of the cystic duct, as well as to the hepatic duct proper which extends a few sections from this surface at the level of the ventral pancreas.

In a 6 mm. embryo the ventral pancreas extends caudalward and to the right of the mid-line of the gut. The common duct has lengthened, and gives rise to the cystic duct which extends ventrally.

A 10 mm. embryo shows great growth of the duct system. The common duct, as well as the dorsal pancreatic duct, arises from the dorsal surface of the gut. A short distance from its origin the common duct gives off caudally the ventral pancreatic duct, then turns cranialward and gives off hepatic ducts in all directions. Beyond this region it divides into two, a small left and a large right duct, from the ventral surface of which a long cystic duct extends ventrally and to the left. From the anterior end of the two hepatic ducts smaller ducts pass outward giving off trabeculae. Some of these smaller ducts projecting medially from the two larger ducts anastomose.

36. *Graphic reconstruction of the cranial nerves of the common garter snake.* W. A. WILLARD, University of Nebraska, College of Medicine.

37. *Specimens showing the differentiation of angioblasts, the method of the formation of the lumen of blood-vessels and the differentiation of red-blood-cells as made out in the living chick.* FLORENCE R. SABIN, Johns Hopkins Medical School.

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- LOEB, HANAU WOLF, A.M., M.D., Professor and Director of the Department of the Diseases of the Ear, Nose and Throat, *St. Louis University, 537 North Grand Avenue, St. Louis, Mo.*

- LORD, FREDERIC P., A.B., M.D., Professor of Anatomy, *Dartmouth Medical School, Hanover, N. H.*
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- MCCLURE, CHARLES FREEMAN WILLIAMS, A.M., Sc.D. (Vice-Pres. '10-'11. Ex. Com. '12-'16), Professor of Comparative Anatomy, *Princeton University, Princeton, N. J.*
- MCCORMACK, WILLIAM ELI, M.D., Adjunct Professor of Anatomy, University of Louisville, Medical Department, *101 W. Chestnut Street, Louisville, Ky.*
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- McFARLAND, FRANK MACE, A.M., Ph.D., Professor of Histology, Leland Stanford Junior University, *2 Cabrillo Avenue, Stanford University, Calif.*
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- McJUNKIN, F.A., M.A., M.D., Professor of Pathology, *Marquette University, School of Medicine, Milwaukee, Wisconsin.*
- McKIBBEN, PAUL S., Ph.D., Professor of Anatomy, *Faculty of Medicine, Western University, London, Ontario, Canada.*
- McMURRICH, JAMES PLAYFAIR, A.M., Ph.D., LL.D. (Ex. Com. '06-'07, '17, Pres. '08-'09), Professor of Anatomy, University of Toronto, *75 Forest Hill Road, Toronto, Canada.*
- McWHORTER, JOHN E., M.D., Worker under George Crocker Reséarch Fund, College of Physicians and Surgeons, *Columbia University, 205 West 107th Street, New York, N. Y.*
- MAGATH, THOMAS BYRD, Ph.B., M.S., Ph.D., Instructor in Anatomy, *University of Illinois, College of Medicine, Chicago, Ill.*
- MANGUM, CHARLES S., A.B., M.D., Professor of Anatomy, *University of North Carolina, Chapel Hill, N. C.*
- MALONE, EDWARD FALL, A.B., M.D., Associate Professor of Anatomy, *University of Cincinnati, College of Medicine, Station V, Cincinnati, Ohio.*
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- METHENY, D. GREGG, M.D., L.R.C.P., L.R.C.S., Edin.—L.F.P.S., Glasg., Assistant Professor of Anatomy, Jefferson Medical College, *11th and Clinton Streets, Philadelphia, Pa.*
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- MYERS, JAY A., M.S., Ph.D., Instructor in Anatomy, *Institute of Anatomy, University of Minnesota, Minneapolis, Minn.*
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- O'DONAGHUE, CHARLES H., D.Sc., F.Z.S., Senior Assistant in Zoology and Comparative Anatomy, *University College, Gower St., London W. C., England.*
- OSTERUD, HJALMAR L., A.B., A.M., Teaching Fellow in Anatomy, *Institute of Anatomy, University of Minnesota, Minneapolis, Minn.*

- OTT, MARTIN D., A.B., Fellow in Anatomy, *University of Minnesota, Institute of Anatomy, Minneapolis, Minn.*
- PAINTER, THEOPHILUS S., Ph.D., Adjunct Professor of Zoölogy, *School of Zoölogy, University of Texas, Austin, Texas.*
- PAPANICOLAOU, GEORGE, Ph.D., M.D., Instructor in Anatomy, *Cornell University Medical College, New York City.*
- PAPEZ, JAMES WENCESLAS, B.A., M.D., Professor of Gross Anatomy and Neurology, *Atlanta Medical College, Atlanta, Ga.*
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- PATTEN, WILLIAM, Ph.D., Professor of Zoölogy, *Dartmouth College, Hanover, N. H.*
- PATERSON, A. MELVILLE, M.D., F.R.C.S., Professor of Anatomy, *University of Liverpool, Liverpool, England.*
- PATTERSON, JOHN THOMAS, Ph.D., Professor and Chairman of the School of Zoölogy, *University of Texas, University Station, Austin, Texas.*
- PFEIFFER, JOHN A. F., M.A., M.D., Senior Assistant Physician and Pathologist, *Government Hospital for the Insane, Washington, D. C.*
- PIERSOL, GEORGE A., M.D., Sc.D. (Vice-Pres. '93-'94, '98-'99, '06-'07, Pres. '10-'11), Professor of Anatomy, *University of Pennsylvania, 4724 Chester Avenue, Philadelphia, Pa.*
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- POTTER, PETER, M.S., M.D., Oculist and Aurist, *Murray Hospital, Butte, Montana, 411-413 Hennessy Building, Butte, Montana.*
- POYNTER, CHARLES W. M., B.S., M.D., Professor of Anatomy, *College of Medicine, University of Nebraska, Omaha, Neb.*
- PRENTISS, H. J., M.D., M.E., Professor of Anatomy, *State University of Iowa, Iowa City, Iowa.*
- PRYOR, JOSEPH WILLIAM, M.D., Professor of Anatomy and Physiology, *State College of Kentucky, 261 North Broadway, Lexington, Ky.*
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- RANSON, STEPHEN W., M.D., Ph.D., Professor of Anatomy, *Northwestern University Medical School, 2431 Dearborn Street, Chicago, Ill.*
- RASMUSSEN, ANDREW T., A.B., Ph.D., Instructor in Neurology, *Institute of Anatomy, University of Minnesota, Minneapolis, Minn.*
- REAGAN, FRANKLIN P., Ph.D., Procter Fellow in Comparative Anatomy, *Princeton University, Princeton, N. J.*
- REED, HUGH DANIEL, Ph.D., Assistant Professor of Zoölogy, *Cornell University, McGraw Hall, Ithaca, N. Y.*
- REINKE, EDWIN, Ph.D., Associate Professor of Zoology, *Vanderbilt University, Nashville, Tenn.*

- RETZER, ROBERT, M.D., Associate Professor of Anatomy, University of Pittsburgh, *Anatomical Laboratories, University of Pittsburgh, Pittsburgh, Pa.*
- REVELL, DANIEL GRAISBERRY, A.B., M.B., Professor of Anatomy, University of Alberta, *Edmonton, Alberta, Canada.*
- RHINEHART, D.A., A.M., M.D., Professor of Anatomy, University of Arkansas, *Old State House, Little Rock, Ark.*
- RICE, EDWARD LORANUS, Ph.D., Professor of Zoölogy, *Ohio Wesleyan University, Delaware, Ohio.*
- RINGOEN, ADOLPH R., A.M., Assistant in Zoölogy, *University of Minnesota, Minneapolis, Minn.*
- ROBERTSON, ALBERT DUNCAN, B.A., Professor of Biology, *Western University, London, Ontario, Canada.*
- ROBINSON, ARTHUR, M.D., F.R.C.S. (Edinburgh), Professor of Anatomy, University of Edinburgh, *The University, Anatomy Department, Edinburgh, Scotland.*
- ROBINSON, BYRON L., A.B., M.A., Teaching Fellow in Anatomy, *Institute of Anatomy, University of Minnesota, Minneapolis, Minn.*
- ROSE, FRANK H., A.B., Austin Teaching Fellow, Department of Anatomy, *Harvard Medical School, Boston, Mass.*
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- SABIN, FLORENCE R., B.S., M.D., Sc.D. (Second Vice-Pres. '08-'09), Associate Professor of Anatomy, *Johns Hopkins University, Medical Department, Baltimore, Md.*
- SANFORD, ELDON WILLIAMS, M.A., Ph.D., Assistant in Anatomy, *Johns Hopkins Medical School, Baltimore, Maryland.*
- SANTEE, HARRIS E., A.M., Ph.D., M.D., Professor of Anatomy, Jenner Medical College, and Professor of Neural Anatomy, *Chicago College of Medicine and Surgery, 2806 Warren Avenue, Chicago, Ill.*
- SCAMMON, RICHARD E., Ph.D., Professor of Anatomy, *Institute of Anatomy, University of Minnesota, Minneapolis, Minn.*
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- SCHULTE, HERMANN VON W., A.B., M.D. (Ex. Com. '15) Professor of Anatomy, *Creighton Medical College, Omaha, Neb.*
- SCHULTZ, ADOLPH H., Ph.D., Collaborator in Embryology, *Carnegie Institution, Johns Hopkins Medical School, Baltimore, Md.*
- SCHMITTER, FERDINAND, A.B., M.D., *Major Medical Corps, U. S. Army, Columbus Barracks, Columbus, Ohio.*
- SCOTT, JOHN W., A.M., Ph.D., Professor of Zoölogy, *University of Wyoming, Laramie, Wyo.*

- SCOTT, KATHERINE JULIA, A.B., M.D., Instructor in Anatomy, Department of Anatomy, *University of California, Berkeley, Calif.*
- SELLING, LAWRENCE, A.B., M.D., *Selling Building, Portland, Ore.*
- SENIOR, H. D., M.B., D.Sc., F.R.C.S., Professor of Anatomy, New York University, and Bellevue Hospital Medical College, *338 East 26th Street, New York, N. Y.* (Middlesex War Hospital, Napsbury, Herts, England.)
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- SHELDON, RALPH EDWARD, A.M., M.S., Ph.D., Professor of Anatomy, *University of Pittsburgh Medical School, Grant Boulevard, Pittsburgh, Pa.*
- SHIELDS, RANDOLPH TUCKER, A.B., M.D., Professor of Histology and Embryology, School of Medicine, *Shantung Christian University, Tsinanfu, Shantung, China.*
- SHUFELDT, R. W., M.D., Major Medical Corps, U. S. A. (Retired), *3356 Eighteenth Street, N. W., Washington, D. C.*
- SILVESTER, CHARLES FREDERICK, Curator of the Zoölogical Museum and Assistant in Anatomy, Princeton University, *10 Nassau Hall, Princeton, N. J.*
- SIMPSON, SUTHERLAND, M.D., D.Sc., F.R.S.E. (Edin.), Professor of Physiology, *Cornell University Medical College, Ithaca, N. Y.*
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- SMITH, GRAFTON ELLIOT, M.A., M.D., F.R.S., Professor of Anatomy and Dean of the Faculty of Medicine, *The University, Manchester, England.*
- SMITH, H. P., A.B., Research Fellow (Hooper Foundation for Medical Research), University of California, *1 St. Geo. Court, East 18th Street, Oakland, Calif.*
- SMITH, J. HOLMES, M.D., Professor of Anatomy, University of Maryland, *Greene and Lombard Streets, Baltimore, Md.*
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- SMITH, PHILIP EDWARD, M.S., Ph.D., Instructor in Anatomy, University of California, *1918 Haste Street, Berkeley, Calif.*
- SMITH, WILBUR CLELAND, M.D., Assistant Professor of Anatomy, *Tulane University, New Orleans, La.*
- SNOW, PERRY G., A.B., M.D., Dean and Professor of Anatomy, *University of Utah Medical School, Salt Lake City, Utah.*
- STEENSLAND, HALBERT SEVERIN, B.S., M.D., Professor of Pathology and Director of the Pathological Laboratory, College of Medicine, Syracuse University, *309 Orange Street, Syracuse, N. Y.*
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- STOCKARD, CHARLES RUPERT, M.S., Ph.D. (Secretary-Treasurer '14-), Professor of Anatomy, *Cornell University Medical College, New York, N. Y.*

- STOTSSENBERG, JAMES M., M.D., Instructor in Anatomy, *Wistar Institute of Anatomy and Biology, Philadelphia, Pa.*
- STREETER, GEORGE L., A.M., M.D., (Ex. Com. '18-), Research Associate in Embryology, *Carnegie Institution, Johns Hopkins Medical School, Baltimore, Md.*
- STROMSTEN, FRANK ALBERT, D.Sc., Assistant Professor of Animal Biology, *State University of Iowa, 943 Iowa Avenue, Iowa City, Iowa.*
- STRONG, OLIVER S., A.M., Ph.D., Assistant Professor of Neurology, *Columbia University, 437 West 59th Street, New York, N. Y.*
- STRONG, REUBEN MYRON, A.B., A.M., Ph.D. (Ex-Com. '16-), Professor of Microscopic Anatomy, *Vanderbilt University Medical School, Nashville, Tenn.*
- SULLIVAN, WALTER EDWARD, A.M., Ph.D., Professor of Anatomy, *Tufts College Medical School, 416 Huntington Avenue, Boston, Mass.*
- SUNDWALL, JOHN, Ph.D., M.D., Professor of Anatomy, *University of Kansas, Lawrence, Kans.*
- SUTTON, ALAN CALLENDER, A.B., M.D., *Johns Hopkins Medical School, Baltimore, Md.* (Abroad as Lieutenant in Medical Officers Reserve Corps.)
- SYMINGTON, JOHNSON, M.D., F.R.C.S., F.R.S., Professor of Anatomy, *Queens University, Belfast, Ireland.*
- SWIFT, CHARLES H., M.D., Ph.D., Instructor in Anatomy, *Department of Anatomy, University of Chicago, 5632 Maryland Avenue, Chicago, Ill.*
- SWINDLE, GAYLORD, Ph.D., Instructor in Anatomy, *Washington University Medical School, St. Louis, Mo.*
- TAINTOR, F. J., M.D., Assistant Professor of Anatomy, *St. Louis University, St. Louis, Mo.*
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- THOMPSON, ARTHUR, M.A., M.B., LL.D., F.R.C.S., Professor of Anatomy, *University of Oxford, Department of Human Anatomy, Oxford, England.*
- THORKELOSON, JACOB, M.D., *Dillon, Mont.*
- THRO, WILLIAM C., A.M., M.D., Assistant Professor of Clinical Pathology, *Cornell University Medical School, 28th Street and 1st Avenue, New York, N. Y.*
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- TODD, THOMAS WINGATE, M.B., Ch.B. (Manc.), F.R.C.S. (Eng.), Professor of Anatomy, *Medical Department Western Reserve University, Cleveland, Ohio.*
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- WARREN, JOHN, A.B., M.D., Associate Professor of Anatomy, *Harvard Medical School, 240 Longwood Avenue, Boston, Mass. (Major Medical Reserve U. S. Army.)*
- WATERSTON, DAVID, M.A., M.D., F.R.C.S.Ed., *Butte Professor of Anatomy, University of St. Andrews, St. Andrews, Fife, Scotland.*
- WATKINS, RICHARD WATKIN, B.S., *Cedar Grove Farm, Granville, Ohio.*
- WATSON, DAVID MEREDITH SEARS, M.Sc., F.Z.S., Lecturer in Vertebrate Paleontology, *University College, Gower St., London W. C., England.*
- WATT, JAMES CRAWFORD, B.A., M.B., Lecturer in Anatomy, *University of Toronto, 20 Hawthorne Avenue, Toronto, Canada.*
- WEED, LEWIS HILL, A.M., M.D., Assistant Professor of Anatomy, *Johns Hopkins Medical School, Baltimore, Md.*
- WEIDENREICH, FRANZ, M.D., a.o. Professor and Prosector of Anatomy, *19 Vogesen Street, Strassburg, i. Els. Germany.*
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- WHEELER, THEODORA, A.B., M.D., *Carnegie Laboratory of Embryology, Johns Hopkins Medical School, Baltimore, Md.*
- WHITE, HARRY OSCAR, M.D., Professor of Anatomy, *Medical Department, University of Southern California, 516 E. Washington Street, Los Angeles, Calif.*
- WHITTENBORG, A. H., M.D., Professor of Anatomy, *College of Medicine, University of Tennessee, 718 Union Avenue, Rogers Hall, Memphis, Tenn.*
- WILDER, HARRIS HAWTHORNE, Ph.D., Professor of Zoölogy, *Smith College, 27 Belmont Avenue, Northampton, Mass.*
- WILLIAMS, JAMES WILLARD, B.A., M.A., Professor of Biology, *College of Yale in China, Changsha, China. (Care of G. H. Malone, Nanking, China.)*
- * WILLIAMS, STEPHEN RIGGS, A.M., Ph.D., Professor of Zoölogy and Geology, *Miami University, Oxford, Ohio.*
- WILLARD, WILLIAM A., A.M., Ph.D., Professor of Anatomy, *University of Nebraska, College of Medicine, 42d Street and Dewey Avenue, Omaha, Neb.*
- WILSON, J. GORDEN, M.A., M.B., C.M. (Edin.), Professor of Otology, *Northwestern University Medical School, 2437 Dearborn Street, Chicago, Ill.*

WILSON, JAMES THOMAS, M.B., F.R.S., Challis Professor of Anatomy, *University, Sydney, Australia.*

WILSON, LOUIS BLANCHARD, M.D., Director of Pathology Division, Mayo Clinic and Mayo Foundation, Professor of Pathology in the University of Minnesota, *Mayo Clinic, Rochester, Minn.*

WISLOCKI, GEORGE BERNAYS, A.B., M.D., Assistant in Anatomy, *Johns Hopkins Medical School, Baltimore, Md.*

WITHERSPOON, THOMAS CASEY, M.D., *307 Granite Street, Butte, Mont.*

WORCESTER, JOHN LOCKE, M.D., Assistant Professor of Anatomy, University of Washington, *Seattle, Washington.*

PROCEEDINGS OF THE AMERICAN SOCIETY OF ZOOLOGISTS

FIFTEENTH ANNUAL MEETING

The fifteenth Annual Meeting of the American Society of Zoologists was held, December 27 and 28, 1917, at the University of Minnesota, Animal Morphology Building, Minneapolis, Minnesota.

BUSINESS SESSION

The business session was called to order by the President, Maynard M. Metcalf, at 2.00 p.m., December 28.

The Secretary being absent, W. C. Curtis consented to serve in this capacity for the meeting.

Election of Members

The following new members were elected upon nomination by the Executive Committee:

- BOYDEN, E. A., Ph.D. (Harvard), Instructor Comparative Anatomy, Harvard Medical School, 61 Clark Street, Newton Center, Mass.
- GUBERLET, J. E., A.M., Ph.D. (Illinois), Professor of Biology, Carroll College, Waukesha, Wis.
- HANCE, R. T., A.B., M.A., Ph.D. (Pennsylvania), Assistant in Zoölogy, University of Pennsylvania, Zoölogical Laboratory, University of Pennsylvania, Philadelphia, Pa.
- HICKERNELL, L. M., A.B., A.M., Ph.D. (Princeton), Assistant Professor of Zoölogy, Syracuse University, 1052 Ackerman Avenue, Syracuse, N. Y.
- HYMAN, L. H., Ph.D. (Chicago), Research Assistant, Chicago University, Hull Zoölogical Laboratory, Chicago University, Chicago, Ill.
- MICHAEL, E. L., A.B., M.S. (California), Assistant Scripps Institution, La Jolla, California.
- PARSHLEY, H. M., A.M., Sc.D. (Harvard), Assistant Professor of Zoölogy, Smith College, 250 Elm Street, Northampton, Mass.
- STREETER, GEORGE L., A.M., M.D., Research Associate in Embryology, Carnegie Institution, Johns Hopkins Medical School, Baltimore, Md.
- YOCUM, H. B., A.B. (Oberlin), M.A., Ph.D. (California), Professor of Zoölogy, Washburn College, 1815 Huntoon Street, Topeka, Kansas.

Election of Officers

The nominations for officers made by the Committee on Nominations (H. V. Wilson, W. E. Kellicott and W. C. Curtis) were unanimously elected.

George Lefevre, for president during the year 1918.

L. L. Woodruff, for vice-president during the year 1918.

M. M. Metcalf, for member, Executive Committee to serve five years.

Report of the Treasurer

The following financial statement submitted by the Secretary-Treasurer, Caswell Grave, was read and accepted subject to its approval by an Auditing Committee consisting of Prof. H. S. Jennings and S. O. Mast.

Receipts during the year, 1917:

Balance on hand January 1, 1917.....	\$649.58
Dues for 1916, (8).....	52.50
Dues for 1917, 13 at 11.50.....	149.50
Dues for 1917, 183 at 7.00.....	1281.00
Dues for 1917, 62 at 5.00.....	310.00
Dues for 1917, 2 at 6.50 Life Members.....	13.00
Dues for 1917, 1 at 4.50 Life Member.....	4.50
Divident (4th) Ind'l. Sav. and Loan Co.....	15.00
Interest at 4 per cent on Saving Bank deposits.....	29.43
Total.....	\$2504.51

Expenditures during the year, 1917:

Express charges.....	\$2.16
Telegram and telephone calls.....	1.55
Stationery, stamps, postcards.....	23.21
Typewriting and clerical assistance.....	20.74
Printing announcements and programs.....	43.25
Loose leaf book for membership index.....	2.75
269 subscriptions for Journals, Wistar Inst.....	1677.00
Total.....	\$1770.66
Balance on hand December 28, 1917.....	\$733.85

Report of Auditing Committee

The Auditing Committee, to which the accounts of the Secretary-Treasurer were submitted in Baltimore January 7, 1918, has made the following report:

Baltimore, Md., January 7, 1918.

We have examined the accounts of the Secretary-Treasurer and find them to be correct.

[Signed] H. S. JENNINGS, S. O. MAST.

RESOLUTIONS

The following resolutions were passed by unanimous votes:

Concerning Time and Place for Annual Meetings

In proposing the resolution concerning affiliations with other biological societies, the Executive Committee made the following statement:

The Executive Committee of the American Society of Zoologists wishes to direct attention to the advantage of frequently holding our mid-winter meetings at the same place with those of other biological societies. We are already affiliated with the American Society of Naturalists and generally meet in the same place with them, having usually one common session for the reading of scientific papers and one or more common social gatherings. We now frequently meet in the same place with others of the biological societies. It is hardly practicable, and probably is not desirable, each year to have all these societies meet in the same city, but it probably could to advantage be arranged to bring a good many of them together each year.

When such a group of societies are gathered in one city, it may sometimes be advantageous to have one or possible more sessions in which two or more of the societies join, and a joint dinner or a common smoker for several or perhaps all of the societies is very pleasant. Yet, on the other hand, it would doubtless be unfortunate to have any organization, or any agreement, that would compel invariably joint sessions or even meeting in the same city.

Your Executive Committee has considered how to secure the advantages of cooperation between the several societies without any interference with the complete freedom of each society each year to follow its own judgment as to place of meeting and nature of program.

Some have suggested having a coordinating society of which we should all be members, but we have felt that this involved probably too much organization. The Physiological, Biochemical, Pharmacological and Pathological Societies have affiliated by a very simple method, namely by having the presidents and secretaries of the several Societies serve together as an executive committee for the affiliated group, it being the intention of these four societies to have a common meeting place and some joint sessions. This plan, while well adapted for a small group of societies studying closely related subjects, might

not work out so well for a larger more diverse group if it implied an obligation for all the societies to meet together. Something still more flexible seems desirable, some arrangement that leaves each society free from any pressure to meet with the group, if, any year, special considerations should make separation advantageous.

We propose for your consideration, and, if it meets your approval, for your adoption, the following plan, namely to have our President and Secretary instructed to consult from year to year with the Presidents and Secretaries of the other biological societies in regard to common meeting place, joint sessions for scientific discussion, joint social gatherings, perhaps some avoidance of simultaneous discussion of the same subject in different societies, and any other matters of cooperation or coordination that may be proposed.

Such consultation between the executive officers of the societies would put no pressure upon any society, but would provide a means for working out so much of cooperation and coordination as may from year to year seem natural and advantageous. It is an arrangement so flexible as not to interfere with the growth of new interests and special affiliations, and yet it provides for the consideration annually of the relations between the societies in their meetings. If from such a consultation there should grow closer affiliation between some of the societies, such as has arisen in the Experimental Biology group, this would still not interfere with the continuance of the plan of general consideration of possible joint arrangements for any one year between a still larger number of the societies. The plan we propose to you seems to give absolute freedom to each society and not even to exert pressure upon any, yet will secure to each a knowledge of the others plans and will provide a means for securing so much of cooperation each year as is desired.

We therefore propose to you the following resolution:—

The American Society of Zoologists would call to the attention of the other professional biological societies the advisability of frequently selecting a common time and place for their annual meetings, and the President and Secretary are hereby instructed to consult with their respective Presidents and Secretaries of the American Association of Anatomists, American Society of Naturalists, the Botanical Society of America, the Ecological Society of America, and The Federation of American Societies for Experimental Biology with the object of accomplishing this purpose for the meetings of 1918. The results of this consultation are to be submitted to the Executive Committee for a final vote. And we further recommend that this report be brought again to the Society at its next annual meeting with a view to its adoption as a permanent policy.

We would call attention to the fact that passing this resolution does not change our relation to the Society of Naturalists, nor would passing of a similar resolution by an other society interfere with any affiliations it may already have formed.

The Society will note that our present By-Law 2, c contemplates just such action as is now recommended. Defining the duties and privileges of the Secretary-Treasurer, it says: "Whenever the proper officers of a number of related societies shall have a conference with a view to determining a common time and place for the several annual meetings, he shall act as the delegate of this Society." Our present Secretary suggests including also the President of the Society in this conference, to conform to the plan of the Federation for Experimental Biology, and this suggestion has been embodied in our report.

The Society, on the motion by Mr. Lefevre, directed that a copy of this resolution be carried to the American Society of Naturalists in session at Pittsburgh.

Concerning the Life and Work of Franklin Paine Mall

During the year just closing death has called from our ranks the genial and able anatomist and embryologist Franklin Paine Mall.

In his death American science has lost one of its eminent devotees.

Always true to the highest ideals of the investigator and teacher he endeared himself to all who were fortunate enough to become acquainted with him. His labors have been ended but the influence of his numerous publications and the excellence of his work will continue.

In memory of his worth as a man and a scholar and in recognition of his devotion and contribution to Zoology we inscribe these minutes in the permanent records of the Society.

This resolution was passed by a rising vote.

Endorsement of Work of the Wistar Institute

The American Society of Zoologists heartily endorses the existing arrangement regarding the Journals published by The Wistar Institute and expresses its thanks and appreciation for the services rendered through the Bibliographic Card System.

Concerning the Biological Station at Fairport, Iowa

The American Society of Zoologists, assembled in Minneapolis, having learned of the recent destruction by fire of the laboratory of the Biological Station at Fairport, Iowa, extends its sympathy to the U. S. Bureau of Fisheries, and expresses the earnest hope that means will be found for the early restoration of the building and the resumption of the valuable work of the Station.

Of Appreciation for the Hospitality of the University of Minnesota

The American Society of Zoologists thanks the University of Minnesota and the local committee for the cordial reception and many attentions incident to the meetings in Minneapolis December 27 and 28, 1917. The Secretary of the society is hereby instructed to forward copies of this resolution to President Burton and to the chairman of the local committee, Prof. H. F. Nachtrieb.

In regard to fisheries

WHEREAS, the new economic conditions relating to the nation's food supply brought upon us by the world-war, make it vitally important that there should be a more thorough development, a greater utilization, and a more intelligent conservation of our fishery resources, and

WHEREAS, the Federal Government maintains more than sixty Agricultural Stations, each liberally equipped with materials, funds and men engaged in investigation and experimentation in the interests of agriculture, and

WHEREAS, the Federal Government has as yet only one or two very poorly equipped and cheaply conducted stations at which investigation and experimentation in the interests of agriculture may be carried on, therefore be it

Resolved by the American Society of Zoologists, that the Congress be requested to provide an adequate number of Fisheries Experiment Stations, equipped with material, funds and expert and practical personnel to do for the products of the seas, rivers and lakes what the Agricultural Experiment Stations and the Department of Agriculture are doing so well for the products of the land."

In regard to problems of North Pacific

WHEREAS, the world-war has brought home to us as never before a realization of the necessity of full and accurate knowledge of our food resources and the necessity of developing and utilizing these resources to the maximum extent compatible with their adequate conservation, and

WHEREAS, our knowledge of the fishery resources of the North Pacific is very imperfect and wholly inadequate to serve as a basis for trustworthy conclusions as to the extent and permanence of these resources, or as to what is necessary for their preservation, therefore, be it

Resolved by the American Society of Zoologists that the proper department or departments of the United States Government be urged to take such steps as may be necessary to provide for a comprehensive and thorough exploration of the Pacific with a view to the development,

greater utilization, and adequate conservation of its fishery resources of whatever kind, and that, if possible, such exploration be undertaken in co-operation with other governments possessing territory bordering the Pacific Ocean.

Symposium

At the session held at 2.00 p.m., Friday, December 28, a symposium on the subject, "The Value and Service of Zoological Science" was held with papers as follows:

1. Utilitarian Values, by F. M. Guyer.
2. Philosophical Values, by W. E. Ritter.
3. Value to the Individual, by H. B. Torrey.
4. Spiritual Value, by W. C. Curtis.

Arrangement will be made for the publication of these papers.

Presidential Address

The address by the President of the Society, Maynard M. Metcalf, on the subject, "Darwinism and Nations," will be published in *Science*.

Exhibits

The following exhibits were made in room 201 in the Animal Morphology building.

1. Drawings illustrating the Anatomy of the Tubinares. R. M. Strong, Vanderbilt University Medical School.
2. Rabbit with Abnormal Eye Showing the Result of Maternal Antiserum Treatment. M. F. Guyer, University of Wisconsin.
3. The Effect of Removal of Eye-stalks upon Body Color in *Cambarus*. Charles Zeleny, University of Illinois.
4. Animal Parasites. Franklin D. Barker, University of Nebraska.

Papers Read

At sessions held during the forenoon and afternoon of Thursday, December 27, and the forenoon of Friday, December 28, papers listed on the program were read, eighteen in full, twenty-three by title.

Abstracts

Abstracts of all papers accepted for the program are printed as part of the proceedings of the meeting.

ABSTRACTS

1. *The olfactory organs of a Coleopterous larva.* N. E. McINDOO, Bureau of Entomology, U. S. Dept. Agriculture.

Up to date the writer has described the olfactory pores in Hymenoptera, Coleoptera, and Lepidoptera. As yet no olfactory organs in any larval insect have ever been described, although it is generally supposed that larvae can smell. Since all larvae are more or less selective in regard to their food which constantly emits odors, it would seem that larvae should have organs to receive these odors. The present papers deals with the morphology of the olfactory pores in the larva of the "fig-eater," *Allorhina (Cotinis) nitida* L. Olfactory pores were found on the antennae, on all the mouth parts, on the thorax at the bases of the legs, and on the legs. The total number varies from 1254 to 1413, with 1359 as an average, which is about equal to that of an adult beetle of the same species. With one exception, the structure of these olfactory pores is similar to that of those found in adult beetles. In the larva the single olfactory organs are widely scattered on all the parts above enumerated, but the compound organs are found only on the distal halves of the last antennal segments. A compound organ consists of a group of closely compact olfactory cells and a thin chitinous plate which bears a pore aperture for each sense cell. On an average, a larva has 25 compound organs whose pore apertures number 625. The antennae of this larva have no sense organs other than the single and compound olfactory organs and tactile hairs.

2. *The relation of the thyroid gland to regeneration in Rana pipiens.* BENNET M. ALLEN, University of Kansas.

These experiments involved three classes of tadpoles: 1. Tadpoles from which the thyroid gland had been extirpated—absence of thyroid secretion. 2. Normal control tadpoles. 3. Tadpoles to which thyroid extracts were fed—excess of thyroid materials.

In each case approximately the terminal half of the tail was removed. Regeneration proceeded normally in quantity and in quality of all three groups. There was a certain amount of individual variation in the degree of regeneration, dependent upon the amount of material removed, the age, and upon individual factors, but the range in amount of regeneration was proportional in all three classes. The tadpoles used ranged in total length from 16.7 mm. to 58 mm. Class 3 was composed of tadpoles of intermediate size, ranging from 32.8 mm. to 45.1 mm. The amount of regeneration in this group was nearly proportional to that in corresponding controls, in spite of the fact that the thyroid feeding had caused a marked shrinkage in body length and had caused one-half of the specimens to develop to the

stage where one or both of the fore limbs had broken through the skin. We conclude from these experiments that the thyroid gland does not influence the process of regeneration.

3. *Modifications produced in uterine young by treatment of the mother with specific antiserum.* M. F. GUYER, University of Wisconsin.

Fowls repeatedly injected with rabbit lenses yielded a serum which when injected into pregnant rabbits attacked the lenses of some of the uterine young, though apparently without effect on the lenses of the mothers. Similar results were obtained in mice. The affected lenses were rendered opaque or liquid. The most striking case is that of a male rabbit which though now adult still has a greatly dwarfed and opaqued left eye. This animal will be exhibited.

4. *Extirpation of the thymus gland in Rana pipiens larvae.* BENNET M. ALLEN, University of Kansas.

The thymus-gland anlagen were removed at their very inception, 8 mm. to 9 mm. tadpoles. This was accomplished by cutting into each side of the head with a cataract needle. Although the severity of the operation retarded development for a time, recovery was rapid and complete. Seven specimens were reared to the time of metamorphosis, attaining normal size and appearance. All died or were killed at this time. It is impossible from the material at hand to determine whether the high mortality at this time was due to the absence of the thymus gland or to other causes. It was in sharp contrast to the fate of the controls. Further experiments will be made upon this point next year. They appeared to be structurally normal in every regard. The characteristic features of metamorphosis occurred. A careful study of the thymus-gland region of each specimen showed that the glands had in each case been successfully removed. Five out of the seven were males. Sexual differentiation was complete, and measurements showed the gonads to be altogether normal in size as compared with metamorphosed controls. A comparison of sections of the gonads of operated and control specimens showed those of both to be identical in structure and in the developmental stage reached by the germ cells.

5. *The influence of thyroid and hypophysis removal upon general body growth and upon the development of the limbs of Rana and Bufo.* BENNET M. ALLEN, University of Kansas.

From a large number of tadpoles of these two types the thyroid gland was removed, while from others the anterior lobe of the hypophysis was removed. In both species the removal of either of these glands caused the development of the limbs to be very greatly retarded from the time of their first appearance. In *Rana pipiens* removal of the hypophysis caused a marked retardation of general body growth, to which a corresponding retardation of limb growth was closely correlated. These tadpoles finally attained a total length

of 48.9 mm. and a hind-leg length of 1.48 mm. This was in marked contrast to the continued growth of the general body dimensions and of corresponding hind-limb length in thyroidless tadpoles of this species. In *Bufo lentiginosus* the results were not so divergent. The removal of the anterior lobe of the hypophysis early caused a color change from black to golden yellow. The absence of either gland caused retardation in limb development. Tadpoles deprived of the anterior lobe of the hypophysis reached a length far in excess of that reached in normal tadpoles. The limbs grew to about three-fifths the length attained in normal toads at metamorphosis. Thyroidless specimens grew somewhat larger than the foregoing, reaching a length of trunk almost twice that of normal toads at metamorphosis, while the hind legs and fore legs grew to a length greater than found in normal toads at metamorphosis. In none of the operated tadpoles did the fore limbs break through the skin.

6. *Functional and rudimentary spermatozoa of rotifers* (illustrated with lantern). D. D. WHITNEY, University of Nebraska.

The later stages in the spermatogenesis of the marine rotifer *Brachionus mulleri* have been carefully reexamined and two interesting additional facts discovered. The normal and rudimentary spermatid cells occur in the ratio of 2:1. By staining with Delafield's haematoxylin, a coarse network of chromatin-like material can be seen in both the normal and the rudimentary cells. This would seem to indicate that in the spermatocyte division some of the chromatin material passes into both kinds of cells. As the normal cells develop and mature into the ripe spermatozoa, the heads become very large and somewhat rounded in shape, but all remain attached to a common central tissue and may form one or more clusters of spermatozoa. The long, vigorous tails have very weak connections with the heads, and when a male individual is slightly compressed under a cover-glass the tails become detached from the heads and may be extruded from the body. If the males are further compressed the heads are also extruded. The tails are capable of swimming around in the culture water for a considerable length of time, and were formerly considered to be the entire spermatozoa. The smaller rudimentary cells at first resemble in form the normal cells, but as they develop such produce a short immotile and tail-like process somewhat spindle-shaped at one end of the cell. This process normally becomes detached from the larger part of the cell while in the testis and may be readily seen inside of a living uncrushed male. These small detached spindle-like bodies were formerly considered to be the complete rudimentary spermatozoa. No chromatin-like material, however, can be demonstrated in these bodies, but a considerable quantity can be seen in the other and larger portions of these cells from which these immotile bodies have become detached. Consequently these bodies cannot be the entire rudimentary sperm cells, but are probably to be regarded as rudimentary tails of the rudimentary sperm cells.

7. *Irregular rate of division of Ameba.* A. A. SCHAEFFER, University of Tennessee.

Amoeba proteus, *A. discoides*, and *A. dubia* were individually pedigreed for a large number of generations, a record being kept of all the progeny from the single individual fathering the pedigree. The division rate is perfectly irregular, varying from two or three divisions in twenty-four hours to only one division in eight or more days. The progeny of the rapidly dividing and of the slowly dividing do not indicate by their subsequent divisions their previous rate of reproduction. The rate of reproduction of unequal-sized sisters and of their immediate progeny was not influenced by the size of the sisters, but only a very few cases of this kind were observed. It seems as if some material which has an influence on the rate of reproduction is unequally divided during the division process. Multinuclear individuals were frequently observed. The amebas remained quite normal throughout most of the experiments.

8. *Opalina and the origin of the Ciliata.* M. M. METCALF, Orchard Laboratory.

Opalina characters—1) reproduces by both longitudinal [Flagellata] and transverse [Ciliata] fission; 2) sexual act complete fusion of dissimilar gametes [Flagellata]; 3) no kinetic center (centrosome) [unique]; 4) kinetoplasm in form of basal granules of the cilia and a network of neural fibrillae connecting these [Ciliata]; 5) uninucleate at sexual period, pleurinuclate during the rest of life cycle [unique]; 6) in pleurinuclate condition all nuclei alike; 7) in each nucleus trophochromatin and idiochromatin distinct (except in origin); in the binucleate species the trophochromatin is in massive chromosomes of constant, definite form and number, apparently equal in number to the granular idiochromosomes, and their division in mitosis is regular; in the multinucleate species the trophochromatin masses are not constant in number, size, or form, and divide irregularly in mitosis; the trophochromatin is extruded from the nuclei at the sexual period; (8) the pseudopleurinuclate condition is due to temporary suppression of the divisions of the body, the nuclei having divided; 9) this delay in completion of mitosis affects also the nuclei, which in numerous species do not complete their division promptly, but come to 'rest' in different stages of the incomplete mitosis. In the sixty (?) species studied, forty (?) of them new, a complete series is seen from uninucleate forms with nucleus in an anaphase of mitosis, through uninucleate species with telophase nuclei, binucleate species with resting nuclei of the usual type, binucleate species with two prophase nuclei, still others with two telophase nuclei, quadrinucleate species, multinucleate species, and finally an elongated multinucleated species whose transverse body divisions have started, but are arrested while incomplete, giving an appearance of metamerization. The binucleate *Opalines* form a genus, *Protoopalina*, distinct from the multinucleate species, *Opalina* proper, the chief distinctions being in nuclear charac-

ters. The Opalinidae are an offshoot from the primitive Ciliata before the latter had acquired true binuclearity and the subsequent dimorphism of nuclei. They should be classed as Portociliata, under the Ciliata. The Astommata (Discophrya, Anoplophrya, Hoplitophrya, etc.) are Euciliata, having arisen much later, after the dimorphic nuclei were acquired. They are not closely related to the Opalinidae.

9. *Full-eye and emarginate-eye from bar-eye in Drosophila without change in the bar gene.* CHARLES ZELENY, University of Illinois.

In the course of selection experiments for high-facet number in the sex-linked bar-eyed stock of *Drosophila*, full-eyed individuals have been produced which are somatically indistinguishable from wild ones. These full-eyed flies are genetically of two very distinct types. One type is the result of a reverse mutation involving the return of the bar gene to the original full-producing condition. Its hereditary behavior is similar to that of the wild *Drosophila* in all the tests that have been made. Such flies have already been described by May. The other type retains the bar gene unchanged, the somatic appearance of full-eyed being due to the formation of a modifying gene outside of the sex-chromosomes. This new gene acts as a recessive factor, since it is without somatic effect in single dose. It is effective in producing full-eye when present in double dose in females heterozygous for the bar gene. Such full-eyed females when crossed with full-eyed males produce males half of whom are low bar and females half of whom are heterozygous bar. In males with the bar gene and in females homozygous for the bar gene, the double dose of the new gene produces an eye which is nearly full, but which differs from full in the presence of a defect at the anterior margin. Such an eye may be designated by the term 'emarginate.' 'Emarginate' females when crossed with full wild males give males all of whom are low bar and females all of whom are heterozygous.

10. *Genetic relation of winged and wingless forms to each other and to the sexes in the aphid Macrosiphum solanifolii.* A. FRANKLIN SHULL, University of Michigan.

In the greenhouse, since the experiments began, this species has passed through the sexual phase three times. In two of these periods every individual either was sexual or produced only sexual progeny in the immediately following generations, so that the experiments could be continued only by hatching the fertilized eggs. In the third, only two parthenogenetic females were left, toward the end of the sexual phase, to continue the line.

During the parthenogenetic portion of the cycle, the frequency with which winged females appeared was very variable, often with a steadily progressive change in their frequency. At any one time, however, wingless mothers produced many more winged offspring than did winged mothers. On the average, winged mothers produced chiefly

wingless offspring, while wingless mothers produced chiefly winged offspring.

During the sexual phase, winged mothers produced chiefly sexual females, while wingless mothers produced chiefly males. The males often appeared mostly near the end of their respective families.

11. *Parthenogenesis and inheritance in grouse locusts.* ROBERT K. NABOURS, Kansas Agricultural College Experiment Station.

Persistent efforts at crossing forms of *Paratettix* (sp.?) with the forms of another apparently closely related group (genus?) have so far failed. However, it has been discovered that the ♀♀ of the latter group (genus?) may reproduce parthenogenetically, the offspring in such instances being exclusively ♀♀. Some of these have now arrived at the third parthenogenetic generation, in considerable numbers, never having been exposed to males of any kind. After producing parthenogenetically a batch, or more, all exactly like herself, a homozygous ♀, if then mated with a homozygous ♂ of a different color pattern gives offspring of the expected uniformly intermediate pattern, with ♂♂ and ♀♀ in approximately equal numbers. Heterozygous ♀♀ partheolgenetically produce ♀ offspring about half showing the pattern of the ♂ grandparent and half the pattern of the ♀ grandparent, with occasional non-disjunction, which is not uncommon in this group.

12. *The winter cycle of egg-production.* H. D. GOODALE, Massachusetts Agricultural Experiment Station.

The winter cycle of egg production was first described by Pearl, whose evidence is all mass evidence. No criteria by which the presence or absence of the cycle could be recognized in the individual have been presented. Pearl finds, furthermore, that the winter cycle is a normal part of the egg production of most Barred Plymouth Rocks. A detailed study of the problem in our Rhode Island Reds shows—

First.—The best criterion of the existence of a winter cycle is the presence of a pause in production, usually ten days or over in length, which follows an egg-laying period of considerable length, the pause beginning, as a rule, in January or February. Rate of production, as shown by monthly production, does not furnish a satisfactory means of recognizing the cycle.

Second.—Many Rhode Island Reds lack the winter cycle, i.e., lay without interruption throughout the winter.

Third.—The character is probably inherited, for some families exhibit the cycle while others lack it. The evidence points to the simple Mendelian formula as the mode of inheritance.

13. *A pedigreed strain of 'twin' Oxytricha.* J. A. DAWSON, Osborn Zoological Laboratory, Yale University. (Introduced by L. L. WOODRUFF.)

There appeared, on July 27, 1917, in a six-day-old stock culture

from a pedigreed race of *Oxytricha*, several pairs of apparently fused animals. These were isolated and from them pedigreed strains of double or 'twin' animals have been carried, thus far, for over one hundred generations, twin producing twin in each generation.

The two cells forming a 'twin' are closely and firmly fused *dorsally*, though the anterior ends are very slightly separated. The 'twins' swim actively with a characteristic rapid rotation on their long axis. The normal single animal of the race from which the 'twin' strain was derived has the macronucleus in two portions, as is usual in the genus *Oxytricha*, but no demonstrable micronuclei. Cytological study of the 'twins' shows simply a doubling of the normal characteristics.

Reproduction of 'twins' is by transverse fission, and has given, in certain cases, as high as 100 per cent of 'twin' progeny for five generations. Occasionally a 'twin' separates into two single animals, which are normal in every respect, except that the anal ends, where separation occurs, retain for an hour or so pointed projections. 'Twins' which show a slightly more marked separation at the anterior end form, when transverse fission takes place, two normal single animals from the anterior end and one 'twin' from the posterior end. Normal single animals resulting from 'twins' continue to divide as usual. The division rate of the 'twin' strain is equal to, or slightly greater than, that of the race of normal animals from which it arose. The proportion of the animals remaining 'twins' seems to be increasing as the strain grows older. The 'twins' of the present generation are apparently identical in structure with those which originated the strain.

A morphological and physiological study of this 'twin' strain is in progress.

14. *Selection for high-facet and for low-facet number in the bar-eyed race of Drosophila.* CHARLES ZELENY, University of Illinois.

In the sex-linked bar-eyed race of *Drosophila*, selection for high-facet and for low-facet number is effective. Crosses show that the modifying factors involved are not sex-linked. The effect of selection therefore cannot be due to differences in the bar gene, either pre-existent or produced during the course of selection. Nor can it be due to modifying genes in the sex chromosomes. Genes in the autosomes must therefore be responsible. That some of these genes appeared before the beginning of the present experiment is indicated by the pronounced effect of the first selections. That others are appearing during its progress, at least in some of the lines, is indicated by the continued effect of selection through many generations in these lines. There are also changes of greater degree involving a return at one step to the full-eye. These are of two distinct types: one, an autosomal change like those responsible for the smaller increases in facet number and the other a return of the bar gene itself to the original wild condition. It is evident that in this one experiment three separate conditions contribute to the effectiveness of selection for high-facet number: first, the differences in accessory

autosomal genes present at the beginning of selection; second, the new autosomal genes arising during the course of selection, and, third, the mutations in the bar gene.

15. *Relative effectiveness of food and other conditions in the production of males in the rotifer, Hydatina senta.* A. FRANKLIN SHULL, University of Michigan.

In a previous paper upon oxygen as a factor in the production of males the actual presence of an excess of oxygen in the water was not demonstrated, though it was necessary to assume from the conditions of the experiments that additional oxygen was dissolved. The amount of oxygen in water similarly treated has now been measured, and compared with untreated water, and with water in which *Euglena* was reared.

The former experiments have been in substance repeated upon several lines with some variability in the results. In some lines the increase in male-production in the presence of oxygen was again demonstrated. One line showed practically no effect of oxygen. Whether this line responds to oxygen in other ways is still under investigation. None of the lines produced more males in the control than in the oxygenated water.

At the same time, controls which were fed upon *Euglena* were maintained. The production of males was increased considerably more in these than in the oxygen cultures, though in no case were the results as striking as those obtained by Whitney, who used *Chlamydomonas* as food. If all the excess of male-production in the *Euglena* experiments not attributable to oxygen was due to food, as is fairly to be assumed, food is a much more potent factor in male-production than is oxygen.

Oxygen appears to increase male-production a little more than creatin, of the greatest concentration that may be safely used, reduces it. *Euglena* increases male-production a little more than manure solution, of the concentration commonly used in food cultures, decreases it.

16. *Concerning the summer plumage of the drake.* H. D. GOODALE, Massachusetts Agricultural Experiment Station.

Some ducks, such as the Gray Call, Mallard and Rouen, molt early in the summer (June). The new plumage, called the summer plumage, is entirely unlike the old, since it strongly resembles that of the female. If the testes of the male are completely removed, the change in color no longer occurs, although the birds molt. Further studies of the problem show that, potentially, the change in color of the intact male takes place two or three months prior to the actual change, for the potential change, at will, may be rendered actual by removing feathers and thus inducing a growth of new ones. The new feathers that come in late in the winter are like the old, but those pulled a little later (March) are like the summer plumage. This change coincides approximately with the beginning of manifestations of sexual activity.

It has also been found that about the time the summer plumage reaches its height, sexual activity diminishes or disappears. At this time the reproductive system of the male contains few or no spermatozoa. The summer plumage no sooner reaches its height than the change back to the breeding plumage begins.

It is apparent, therefore, that the summer plumage develops coincidently with the period of greatest activity of the testes, while the breeding plumage, so-called, develops during the quiescent period.

The histological changes in the testes are being examined.

17. Functional inertia in the movement of Ameba. A. A. SCHAEFFER, University of Tennessee.

The path of an ameba has character: that is, the direction in which an ameba is moving at any time is influenced by the direction in which the ameba has been moving just previously. The tendency to move in straight paths is not due to mere mechanical inertia of the streaming protoplasm, nor is it due to any form of sense perception known to man. Nor is the tendency to move in straight paths the result of minimal external stimulation or of the absence of external stimulation. Occasionally a slight lateral external stimulus produces a visible response, and yet the original (straight) path is maintained. The encircling of objects, a phenomenon of rather frequent occurrence, may be explained as due to a balance between the effect of functional inertia of movement and the effect of a mild positive stimulus. These conclusions are based on experimental records of a number of species of amebas.

18. Acidosis the cause of death at high temperature. ALFRED GOLDSBOROUGH MAYER, Carnegie Institution of Washington.

Those corals which have the highest rate of metabolism, as measured by oxygen consumption, are the ones that are most readily killed by high temperature, as will appear from the following table:

NAME OF CORAL	CONSTANT TEMPERATURE WHICH IS JUST SUFFI- CIENT TO CAUSE DEATH IF EXPOSED TO IT FOR ONE HOUR	RELATIVE OXYGEN CON- SUMPTION PER HOUR PER GRAM OF LIVING SUB- STANCE OF EACH CORAL
	°C.	
<i>Acropora muricata</i>	34.7	18.7
<i>Orbicella annularis</i>	35.6	6.1
<i>Maeandra areolata</i>	36.8	5.5
<i>Favia fragum</i>	37.05	3.8
<i>Siderastrea radians</i>	38.2	1.0

Moreover, ability to resist high temperature is proportionate to a coral's ability to resist the poisonous effects of carbon-dioxide gas dissolved in seawater. Death in the presence of CO₂ is not due to asphyxiation, for all corals can survive for more than six hours in sea-

water deprived of oxygen under an air pump. Moreover, the death temperature is the same whether the oxygen is 3.0 times the normal or reduced to 0.3 its normal concentration. Thus high temperature does not cause death through asphyxiation, but more probably through the accumulation of acid in the tissues.

19. *An analysis of the respiration of Cassiopea, and the nature of the nervous control of its rate of metabolism.* LEWIS R. CARY, Princeton University.

The oxygen consumption was determined by the Winkler method, using sufficiently large respiration chambers to provide against the reduction of the oxygen tension to a point sufficiently low to interfere with the normal respiration of the experimental material. All experiments were performed upon half disks to avoid the introduction of individual variation, in metabolic activity, which has been found to be very marked in this organism. In a series of experiments devised to determine the respiration of the several tissues of the disk it was found that taking the oxygen consumption of a half disk pulsating under the control of its sense organs as 100 per cent that of the different tissues was as follows:

	per cent
Active muscles.....	36.15
Epithelia (including inactive muscles).....	60.23
Nerves and sense organs.....	1.37
Mesogloea (and bacteria?)	2.25

When the muscles are inactive, the ectodermal tissues of the exumbrella use 60.5 per cent as much oxygen as those of the subumbrella. This figure represents, as closely as it could be determined, the relative mass of protoplasmic tissue in the two epithelia. When the muscular activity of a specimen is taken from nervous control by removing the sense organs and starting a circuit wave of contraction in a labyrinth of the subumbrella tissue, the rate of pulsation can be controlled by the length of the labyrinth so that the rates of the 'active' and 'activated' halves will be the same. Under these conditions, the oxygen consumption is greatest for the active half disk, as is also the rate of regeneration when specimens have been subjected to the same type of operation.

The control of metabolic activity by the nerve centers seems, therefore, to be exercised through the general epithelial covering of the body as well as through the specialized contractile tissues.

20. *The rate of intracellular oxidation in Paramecium caudatum and its relation to the toxic action of KNC.* E. J. LUND, University of Minnesota.

It is generally assumed that the toxic action of KNC upon cells and organisms in general is due to an inhibitory effect of KNC upon intracellular oxidations. This conclusion originates from the experiments on mammals by Geppert (Zeitschr. f. klin. Med., vol. 15, '89) and is

based primarily upon experiments on the effect of KNC on echinoderm eggs by Warburg (Ergeb. d. Phys., vol. 14, '14), Loeb, and others.

Data will be presented which show that the rate of intracellular oxidation in *Paramecium caudatum* is independent of the toxic action of KNC. The oxidations go on at the same rate in cells which are undergoing visible death changes, as in normal cells. Concentrations of KNC varying from M/272 to M/27200 are equally ineffective in inhibiting the normal rate of oxidations. After cytolysis by KNC oxidations apparently cease. It is obvious that conclusions and inferences based on the supposed specific action of KNC on intracellular oxidations in other cells than those where proof of such specific action is given is unwarranted.

21. *The sensory behavior of Chiton.* · LESLIE B. AREY, Northwestern University Medical School.

A comprehensive investigation of the sensory capacity of this generalized mollusc not only promises facts of intrinsically fundamental importance, but also paves the way for future quantitative attacks on problems of general sensory physiology.

This sluggish and seemingly unpromising animal gives surprisingly clear-cut responses to a large variety of sensory stimuli. The effects of touch, light (including shading), temperature, gravity, currents, chemicals, vibrations, etc., have been tested quantitatively and the results analyzed.

22. *Reversals of phototaxis and carbon dioxide production in may-fly Nymphs.* (Lantern.) W. C. ALLEE, Lake Forest College.

The phototactic reactions of a species of may-fly nymphs (Heptageninae) were reversed by treatment with various chemicals. The rate of carbon dioxide production of nymphs experimentally reversed was compared with that of untreated nymphs by means of Tashiro's Biometer with the following results:

Hydrochloric acid (m/25) caused reversals soon after treatment began or after an interval of about 35 minutes. In the first case the animals were stimulated; in the second, they were depressed as indicated by the rate of production of carbon dioxide. These nymphs are normally negative to light. Only 20 per cent of the untreated nymphs give a positive reaction. Such positive nymphs were also reversed by treatment with hydrochloric acid.

Potassium cyanide caused reversals which were always accompanied by depression.

Ethyl alcohol acted in the same way as hydrochloric acid, first stimulating and later depressing, but was not so effective in causing reversals as the other reagents.

Nymphs may be reversed by long exposure to light. This caused an increase in the rate of carbon dioxide production.

In preliminary experiments, with other species of may-fly nymphs, Child's cyanide method gave similar results.

All nymphs that reversed their light reactions were either stimulated or depressed, but stimulation or depression did not necessarily involve reversal.

23. *Tactile reactions of the de-eyed hamlet.* W. J. CROZIER. Bermuda Biological Station.

The de-eyed hamlet (*Epinephelus striatus*) gives well-defined reactions to the near approach of solid bodies. In the seeing fish this sensitivity is present, but motor effects which it might induce are almost completely inhibited. Mechanical deformations in the water, of minute amplitude, are the source of stimulation (not chemical or electrical disturbances). The presence of this exceedingly delicate form of sensitivity, generally distributed over the surface of the fish, and leading to deliberate reactions of a definite character, can (both directly and by differential narcosis) be used to detect the influence of chemical excitants, locally applied, upon the end organs of the tactile sense. Although the existence of this form of irritability vitiates any direct study of the mode of excitation in 'common chemical' sense reactions, it can be clearly demonstrated that the generally distributed 'common chemical' sensitivity of this fish does not involve tactile receptors.

Since the hamlet with well-developed eyes exhibits a high degree of tactile discrimination, such as has been described for the blind cave fishes (Eigenmann), although its existence would be quite overlooked unless blinded animals were studied, it is unnecessary to suppose that the end organs of this form of sensitivity have been determined either by blindness or by life in caves.

24. *The effect of temperature upon facet number in the bar-eyed race of Drosophila.* E. W. SEYSTER, University of Illinois. (Introduced by CHARLES ZELNY.)

In connection with selection experiments in progress in the Zoological Laboratory at the University of Illinois, a study was made of the effect of temperature upon facet number in the unselected bar-eyed race of *Drosophila*. It was found that facet number *decreases* with increase in developmental temperature. In males the average facet numbers were: 165 at 17°, 114 at 22°, and 72 at 28°. In females the numbers were: 140 at 17°, 85 at 22°, and 48 at 28°. This gives for males a decrease of 7.3 per cent per degree between 17° and 22° and of 7.5 per cent between 22° and 28°. The corresponding decreases for females are 9.6 per cent per degree between 17° and 22° and 9.3 per cent between 22° and 28°.

The facet number at 17° is approximately 2.3 times that at 28° in males and 2.9 times in females. The relation is the reverse of that ordinarily given for chemical reactions and may be explained on the assumption that the chemical activity of an inhibitor of facet number is the effective agent concerned.

According to preliminary experiments, the period in which temperature is effective at 28° comes somewhere between 2½ and 4½ days

after the laying of the eggs. At this temperature the larva usually pupates on the seventh day.

25. *The nature of the orienting light stimulus in Vanessa antiopa.*

WILLIAM L. DOLLEY, JR., Randolph-Macon College, Ashland, Va.

Vanessa antiopa, when exposed to two lights of equal intensity the rays of which are at right angles, moves in general toward a point half way between the sources. If, however, one of the lights is made intermittent by placing a revolving sector-wheel in the beam and the illumination in the two beams is equal, the behavior of *Vanessa* is very different. If one-fourth of the wheel is removed, the degree of stimulation of the intermittent light varies, in proportion to its flash-frequency, from 2 to 20 per second. If one-half of the wheel is removed, the effect of this intermittent light is very similar to that described above, except that when the flash-frequency is low the stimulus is stronger than when less of the wheel is removed. If, however, three-fourths of the wheel is removed, although the stimulus of this intermittent light tends to vary in proportion to the flash-frequency, the difference in the effect produced upon the organisms by revolving the sector-wheel slowly and rapidly is not so great as it is when the aperture in the wheel is smaller. Moreover, when the flash-frequency is low, 2, 5, and 10 per second, intermittent light produced by a rotating sector-wheel three-fourths of which is removed is stronger as a stimulus than when less of the wheel is removed. The reverse is true when the flash frequently is high, 20 and 30 per second. These results seem to indicate that the orienting stimulus in light may be due to the continuous action of light. They also show that light may produce orientation through a change of intensity if the flash of light is short enough and if it is not followed by too long a period of darkness.

26. *The relative sensitivity of Volvox to spectral lights of equal radiant energy content.* HENRY LAURENS and HENRY D. HOOKER, JR., Osborn Memorial Laboratories, Yale University.

The physiological effects of spectral lights of equal radiant energy content have been investigated in accordance with the program outlined in a recent paper (Amer. Jour. Physiol., vol. 44, p. 504). Results warranting publication have been obtained so far in one case, namely, *Volvox globator*. Dark-adapted, positive forms were used. The presentation time requisite to initiate a motor reaction was determined for each of the twenty-three lights. The speed of locomotion toward each was determined and compared to the speed of the same individuals toward a white light of the same radiant power. The reactions to white and colored light coming from opposite directions, and the speed of locomotion, were determined and compared to the speed of the same individuals reacting to the white light alone, and to the colored light alone.

The following results have been obtained: All the lights (ranging from 420 $\mu\mu$ to 670 $\mu\mu$) induce positive motor reactions. The most

effective wave-length is in the immediate neighborhood of $494\ \mu\mu$. The curve of relative stimulating value, as shown by the presentation time, is a normal curve of error. When organisms are exposed to white and colored light of equal radiant power coming from opposite directions, they move toward the colored lights of wave-length $574\ \mu\mu$ and less, but away from the colored lights of longer wave-length.

27. *The influence of excessive sexual activity of male rabbits. 1. On the nature of the seminal discharge.* ORREN LLOYD-JONES AND F. A. HAYS.

In general, the plan of the experiment was to couple the male in as rapid succession as possible to 'preliminary' females and then to mate him once to the female from which a litter was desired. Litters of rabbits were obtained and semen studies were made from the fifth, tenth, fifteenth, and twentieth copulations in from one to four hours. Semen was recovered from the females by catheter. The data show a decrease in amount of discharge and in the number of sperm per cubic millimeter as the number of copulations increases. The rate of progressive linear motion of the sperm was determined by the use of the ruled surface of the cytometer and a stop-watch. Sperm move forward in semen diluted nine times with an isotonic solution at a rate of 0.02 to 0.03 mm. per second. It appears that the velocity of those sperm which show the progressive vibratile type of motion is not affected by the number of copulations. But the type of motion is influenced; in semen from the twentieth service there are few 'progressive movers,' and many 'spiral movers' and 'bunters.' The duration of motion was recorded as per cent of sperm active at four-hour intervals after recovery. The sperm from the higher-service groups shows a more rapid decline in the per cent of sperm active. Motility persists longer in semen diluted nine times than in undiluted semen. There is a marked and regular decline in per cent of pregnancies induced as the service number increases. The number of young in the litter was not affected until the twentieth service, when there was a pronounced falling off in litter size.

28. *Further experiments on the transmission of swamp fever.* (Lantern.)

JOHN W. SCOTT, University of Wyoming.

Some important results have been found since reporting on this subject a year ago. We have further proof that swamp fever may be transmitted from sick to well horses by means of *Stomoxys calcitrans*. We now have definite proof that the disease may be transmitted by *Tabanus*. The transmission is a mechanical one, but it is interesting to note that both acute and chronic cases may be produced by such transmission. Mechanical transmission by means of a hypodermic needle contaminated with extremely small amounts of infected blood is sufficient to produce the disease; this indicates that the insect theory of transmission is adequate.

Other facts brought out include the following: Apparent immunity may be developed, and the horse still be a carrier of the virus. Horses suffering a light attack and showing few symptoms may carry virulent

blood, and subinjections from these produce severe cases. Cases produced by subinjections of blood are, as a rule, not so severe as cases reported from the field, but many mild cases are probably overlooked in the field. The disease may be transmitted by infected mares to their sucking colts, as shown by the Japanese Commission. The amount of blood used in subinjection also bears roughly an inverse relation to the length of the subsequent incubation period. Finally, during the progress of the disease, there is a decrease in the total hemoglobin content per cubic centimeter which is approximately proportional to the characteristic decrease in the number of red corpuscles.

29. *Effect of chemicals on reversion in orientation to light in the colonial form, Spondylomorom quarternarium.* S. O. MAST, Johns Hopkins University.

Spondylomorom orients fairly precisely in light. It is negative under certain conditions and positive under others. The effect of chemicals on the sense of orientation was ascertained both by adding minute traces of the substances tested to the solution in which the organisms were exposed to light until it became so concentrated that they no longer reacted and by putting organisms directly from the culture solutions into watch-glasses containing culture solutions with known amounts of chemicals added. The illumination and the temperature were constant throughout each experiment.

The following substances cause negative specimens to become positive: Acetic, carbonic, hydrochloric, nitric, sulphuric, formic, boric, chromic, tannic, tartaric, and oxalic acids, chloroform, ether, and chloral hydrate.

The following substances have no effect on the sense of orientation: sodium, potassium and ammonium hydrates, magnesium sulphate, sodium chlorid, calcium chlorid, potassium nitrate, formalin, sugar, oxygen, hydrogen peroxid, potassium cyanide, and strychnin.

For the following substances the effect is questionable: ethyl alcohol, ammonium chlorid, and distilled water.

The effect of acids is not specifically related with the hydrogen ion-concentration. The culture solution in which *Spondylomorom* lived was continuously fairly strongly alkaline. When a trace of acid is added to such a solution *Spondylomorom* usually becomes strongly positive at once; but it remains positive only a moment, then it becomes negative and remains so. If more acid is now added, it again becomes positive, etc. Tests with neutral red show that *Spondylomorom* may become positive when the solution is still strongly alkaline and that it may still be negative when the solution is neutral or even slightly acid. It consequently appears that if the sense of orientation in this organism is dependent upon either the hydrogen or the hydroxyl ions, it must be dependent upon the time rate of change in the concentration of the ions. However, the fact that chloroform and ether produce the same effect as acids indicates that it is not dependent upon the ions mentioned.

30. *The rate of intracellular oxidation in Paramecium caudatum and its relation to oxygen concentration.* E. J. LUND, University of Minnesota.

Measurements of the oxygen consumption by *Paramecium caudatum* when placed in water containing concentrations of oxygen which vary from those which are toxic (two to three times the oxygen concentration in distilled water at N. T. P.) to about 1/50 of this concentration, show that the rate of oxygen consumption is not affected by varying the concentration between these limits, temperature and other conditions being the same.

31. *Assortive mating in a nudibranch.* W. J. CROZIER, Bermuda Biological Station.

From measurements of the lengths of 148 couples of *Chromodoris zebra* there was found a correlation coefficient = 0.626 for the lengths of two members of a pair copulating in nature. Mass experiments and studies of individual behavior show how this correlation is the result of true assortive mating.

Egg-masses laid by this hermaphroditic mollusc contained 2,300 to 20,000 eggs, depending upon the size of the animal (4 to 18 cm. length). Mutual fertilization is practiced, and one egg-mass is the consequence of each insemination. Assortive coupling leads a) to the conservation of gametes, and directly b) to the fertilization of the greatest number of eggs—as has been ascertained by direct observation; it thus helps to insure the establishment of the largest possible number of larvae.

The assortive conjugation of *Chromodoris* and the adaptive consequences to which this process gives rise are determined in a mechanical way by the structure of the nudibranch. An important instance is thus afforded of the way in which certain types of 'adaptive' behavior are to be explained.

32. *The habits of the yellow perch.* A. S. PEARSE, University of Wisconsin.

Perch in a small, shallow, muddy lake and in a large, clear, deep lake were examined weekly for two years. Food consisted of the following items expressed in volumetric percentages: chironomid larvae, 25; cladocerans, 22; *Corethra* larvae, 6.4; silt and bottom debris, 6; fish, 5.2; amphipods, 3.6; plants, 3.5; *Sialis* larvae, 3.4; caddis fly larvae, 2.1; oligochaetes, 1.5; crayfishes, 1.5; odonate nymphs, 1.4; clams, 1.2; algae, 1.2; snails, 1.1; ephemeropterid nymphs, 0.9; calcium carbonate crystals, 0.5; midges, 0.5; leeches, 0.4; Hemiptera, 0.3; mites, 0.3; midge pupae, 0.2; copepods, 0.1; ostracods, 0.09. There were seasonal variations, but an adult perch ate an amount equal to 7 per cent of its own weight daily. Digestion was thrice as rapid in summer as in winter. Perch are continually moving from place to place, but do not make rapid vertical migrations, except that they move upward somewhat at night. During most of the year they re-

main in deep water, but come in shore to breed in spring when water reaches 7°–10°C., the males preceding the females to the spawning grounds. During late summer and early autumn the perch in certain lakes mostly forsake the stagnant, oxygen-free water near the bottom. They can, however, live for over two hours in such stagnant water, and while in it draw to some extent on the reserve oxygen in the swim bladder.

33. *Reversion in orientation to light in the colonial forms, Volvox globator and Pandorina Morum.* S. O. MAST, John Hopkins University.

Volvox and *Pandorina* react very strongly to light and they orient precisely. Ordinarily they are negative in strong and positive in weak light, but under certain conditions the opposite is true.

The sense of orientation is dependent upon the time of exposure as well as upon the intensity of the illumination. In *Volvox* no definite results were obtained, but in *Pandorina* it was found that in weak light it required a longer exposure to make positive individuals negative than it did in strong light. In strong light, however, it required more energy than it did in weak light, e.g., in one experiment it required 80,000 meter-candle-hours in an illumination of 16,000 meter-candles; 24,000 m.c. hrs. in 4,000 m.c.; 7,000 m.c.hrs. in 1,000 m.c.; 2,000 m.c.hrs. in 250 m.c.; 888 m.c.hrs. in 111 m.c., and 444 m.c.hrs. in 27 m.c.

Under certain conditions a sudden decrease in illumination, e.g., from direct to diffuse sunlight, makes negative colonies positive; but after having been positive in the diffuse light for a moment they may become negative again without any further change in illumination.

The reversion in light is not primarily dependent upon photosynthesis. Red and yellow light, in which photosynthesis is relatively strong, have little effect on reversion in orientation, while blue and green, in which photosynthesis is weak, have an effect nearly as great as white light.

Increase in temperature causes negative specimens to become positive and decrease causes the opposite, but neither the degree nor the extent of change in the temperature is specific in its effect. Under certain conditions, the colonies may be negative or positive in practically all temperatures in which they orient at all.

Alkalis and salts have no effect on reversion, neither in negative nor in positive colonies. Acids and some anesthetics, especially chloroform, cause negative colonies to become strongly positive; but reversion is not specifically dependent upon the concentration of the chemicals. Colonies which are positive in a solution having a given chemical concentration may be negative in the same solution or even in a weaker solution.

The sense of orientation is dependent upon the age of the colonies. Young colonies are more likely to be negative than old ones. In a given solution the young specimens frequently collect at the side of the dish farthest from the light, while the old ones collect at the opposite side.

34. *The total quantity of plankton produced by a lake.* C. JUDAY, University of Wisconsin.

Investigations on lakes in the vicinity of Madison, Wisconsin, show that the larger plankton organisms, those that are readily obtained with the standard silk-gauze net, do not constitute as large a portion of the total plankton, generally, as the smaller organisms which are lost through the meshes of the net and which can be obtained with a centrifuge. The organic matter of the centrifuge plankton varies from a minimum somewhat smaller than the net plankton to a maximum twenty-five times as great; during most of the year the former is three to five times as great as the latter.

35. *On the parasitism of Carboniferous crinoids.* ROY L. MOODIE, University of Illinois, College of Medicine.

While engaged in reviewing the literature of paleontology in the course of a search for paleontological evidences bearing on the antiquity of disease, the writer was interested in noting several cases of parasitism by myzostomid worms in the stems of fossil crinoids. Later several specimens of enlarged crinoid stems from the Carboniferous were loaned for study by the University of Chicago.

Etheridge, in 1880, first called attention to the swollen crinoid stems from the Carboniferous of England. Later, von Graff, in 1885, published a memoir on the deformities of crinoid stems, and showed that the deformities were due to parasitic worms, which had already been suggested by Etheridge. Von Graff published his paper in the *Paleontographica* and illustrated it with an excellent lithographic plate. He reviewed the subject of parasitism of crinoid stems and cited the work of the Challenger expedition on this subject, suggesting that since the deformities of the recent crinoids were usually due to myzostomids that there was no reason to suppose that the fossil deformities were due to any other cause.

John M. Clark has written an excellent paper on the pre-Carboniferous evidences of communism and commensalism, calling his study "The Beginnings of Dependent Life." In his extensive collections he has found no trace of definite parasitism, but certainly the cases described by him may be regarded as the beginnings of parasitism. It seems probable, at present, that true parasitism was not attained until the Carboniferous period.

The specimen of crinoid stems at the writer's disposal show great tumor-like masses, due doubtless to the pathological influence exerted by the parasites. Von Graff found definite evidences of the carbonized remains of the parasite, and referred it to the myzostomids.

In the present instances we are not in a position to say what the parasite was. Section of the material adds little to the facts already described by von Graff, but simply records another instance of parasitized crinoid stems—the first record, so far as can be determined, of parasitism in American fossil crinoids. Unfortunately, the present material has been completely mineralized, so that nothing is left of the original animal structure save its form.

So far as known at present, no fossil animals suffered from disease prior to the Permian when caries of the bone and callus formation are known. However, if we may regard parasitism as a form of disease, we witness in the Carboniferous the very beginnings of disease, which is manifest to-day in such a vast multitude of forms. Diseases, like animals and plants, present certain persistent types, such as caries, pyorrhea, parasitism, necroses, osteoperiotitis, and various arthritides, which arose early, prior to the Cretaceous, and have persisted down to the present in an almost unchanged form.

36. *The Acanthocephala of North American birds.* H. J. VAN CLEAVE, University of Illinois.

But four genera, comprising a total of eight species, of Acanthocephala have been reported from North American birds. Through the U. S. Government Collections the writer has had access to materials containing specimens belonging to four additional genera, which are now reported from North America for the first time. *Corynosoma constrictum* occurs in *Oidemia americana*. *Echinorhynchus rectus* Linton has been reexamined and shown to belong to the genus *Plagiorhynchus*. Another species, *P. formosus*, has been found in *Colaptes auratus*. *Polymorphus obtusus* has been taken from *Anhinga anhinga*.

Mediorhynchus grandis has been assigned to the genus *Heteroplus*. This last genus belongs in the family Centrorhynchidae rather than in the Gigantorhynchidae, as proposed by Kostylew, its founder.

There are, then, a total of thirteen valid species of Acanthocephala known to occur in North American birds. In addition, four species mentioned by Leidy are insufficiently described to permit of their being placed with accuracy in the modern classification.

Among birds the occurrence of two different species of Acanthocephala within the same host individual has never come under observation of the writer, nor has any positive case wherein two different genera have been found in the same species of host.

Further evidence is added in support of the hypothesis that the Acanthocephala parasitic in fresh-water and terrestrial hosts of North American stand as a distinctive fauna. Comparisons of infestations of birds in Europe and in North America shows that in most cases families of birds common to the two continents harbor entirely different genera of Acanthocephala.

37. *The morphology and life history of a new trematode parasite, Lissorchis fairporti* nov. gen., et nov. spec., from the buffalo fish, *Ictiobus*. THOMAS BYRD MAGATH, Department of Anatomy, University of Illinois College of Medicine. (Introduced by ROY L. MOODIE.)

A careful study of the morphology and life history of *Lissorchis fairporti* nov. gen., et nov. spec. has been made. This parasite occurs in about 50 per cent of the experimentally raised buffalo fish (*Ictiobus bubalus* and *Ictiobus cyprinella*) in the ponds at the United States Bureau of Fisheries Biological Station at Fairport, Iowa. It is found

in relatively small numbers per host in the intestine, and there is evidence to show that it has been responsible for the large death rate sometimes noted among buffalo fish during their first summer.

The new genus *Lissorchis* cannot be placed in any of the existing subfamilies, and the new subfamily Lissorchiinae has been created to contain it. The description of the genus is as follows: Distomes; body flattened, elongate, tapering posteriorly and of moderate size. Cuticula covered with small spines; fleshy spines around suckers. Acetabulum powerful and as large or larger than the oral sucker which is also well developed. Prepharynx and esophagus much reduced; intestinal crura not reaching the posterior end. Excretory system Y-shaped, branching anterior to the testes. Genital pore marginal and sinistral, situated below the middle of the acetabulum. Ovary mesial and lobed, no seminal receptacle; Laurer's canal present. Uterus coiled and extending from beyond the genital pore to the posterior tip of the body, filled with small, thin-shelled eggs. Testes ovoid, large, mesial, and unlobed, lying in a straight line with the ovary and posterior to it. Very large seminal vesicle and well-developed cirrus anterior to ectal end of uterus. Vitallaria extending on either side from posterior of acetabulum to half way between posterior tip and acetabulum. Vitallarial sac present and Mehlis' gland large. Habitat: Intestine of fresh-water fishes.

The life history was obtained experimentally and followed to some extent in the field. The cercaria of this form has been described and found in *Planorbis trivolvis*; it belongs to the xiphidiocercaria. Experimentally, it encysted in chironomid larvae after boring through their skin, and when these were fed to buffalo fish the worm was freed from the cyst and developed to stages like those found in nature in infected fish. Observations indicate that the eggs from the adult trematodes hatch in the late fall, live over winter in the liver of *Planorbis trivolvis*, and multiply in sporocysts. In the summer the cercariae find their way to water, infect chironomid larvae, and in turn the buffalo fish when they eat the infected larvae. Fish cannot be infected by directly feeding them with the cercaria.

Note: This paper will appear in the Journal of Parasitology as a contribution from the laboratory of the U. S. Bureau of Fisheries, Fairport, Ia.

38. *Easily available sources of material for the study of animal parasites.* FRANKLIN D. BARKER, University of Nebraska.

Animal parasites afford one of the most interesting and practical groups of animals for study. Their use neglected due to erroneous idea of unpleasantness and difficulty in securing material. Easily available sources are as follows:

Protozoa. 1. *Entamoeba* sp.?, in small intestine of mice. 2. *Sporozoa*: a. *Gregarina*, several species in intestine of grasshopper and cricket. b. *Monocystis agilis*, in seminal vesicles of earth worms. c. *Hemogregarina* sp.?, blood of snakes. 3. *Ciliata*: a. *Opalina*, several species in

cloaca of frog. *b. Nyctotherus* sp.?, species in cloaca of frog. 4. Flagellata: *a. Trypanosoma lewisi*, in blood of rat. *b. Herpetomonas muscae*, in intestine of house fly.

Plathelminthes.—1. Trematoda. *a. Pneumonoecus*, several species in lungs of frog. *b. Amphimerus ovalis*, in bile ducts of soft-shell turtle. *c. Miracidium* stage in eggs of trematodes sp.?, in intestine of frog. *d. Redia* and cercaria stages in liver, reproductive glands, and tentacles of water snails. 2. Cestoda: *a. Taenia serrata*, in intestine of dog. *b. Taenia serialis*, in intestine of dog. *c. Dipylidium caninum*, in intestine of dog and cat. *d. Cysticercus* stage, *Cysticercus pisiformis*, on omentum, mesentery, and intestine of cotton-tail rabbit. *e. Onchosphere* stage in eggs of *Hymenolopis diminuta*, in intestine of rat, also in eggs of gravid proglottids of *T. serrata*.

Nemathelminthes. 1. Nematoda: *a. Ascaris suum*, in intestine of pig. *b. Belascaris marginata*, in intestine and stomach of dog and cat. *c. Ancylostoma caninum* (hookworm), in intestine of dog. *d. Oxyuris ambigua*, in intestine of rabbit. 2. *Acanthocephala*, several species in intestine of turtles and fish. 3. *Gordius* sp.?, in fresh water ponds and ditches.

Arthropoda.—1. Fleas: *a. Ctenocephalus canis*, on hair of dog and cat. 2. Mosquitoes: *a. Culex* sp.?, *b. Anopheles* sp.?—eggs, larva and pupa—in rain barrels and ditches. 3. Lice: *a. Menopon pallidum*, on chickens.

Identification descriptions and drawings are given. Methods of collecting, preserving and mounting are indicated.

Animal parasites may be obtained from Ward's Natural Science Establishment, Rochester, N. Y., and Western Biological Supply Co., Lincoln, Nebr., and other biological supply houses.

39. *The need for extensive oceanographic and biologic explorations in the North Pacific.* WM. E. RITTER, University of California.

The need indicated is both scientific and economic, and would involve an undertaking of such magnitude that nothing less than the National Government would be equal to it. It should really be international and include the United States, Canada, and Japan at least.

Enough is already known about this oceanic area and the organisms inhabiting it to bring out the fact that it presents differences from its nearest of kin, the North Atlantic, so considerable as to make it impossible to apply to it in detail generalizations reached by investigations of the corresponding Atlantic area.

Illustrative of these differences on the oceanographic side may be mentioned the greater size and average depth of the Pacific; its greater isolation from the Arctic Ocean; its much more fully developed phenomenon of upwelling water; its simpler and less sharply defined system of currents; the relative paucity, so far as the North American continent is concerned, of incursion of fresh water into the Pacific; and finally the somewhat lower specific gravity of North Pacific water.

On the biological side, illustrative differences are seen in the rela-

tively meager development of a Pacific sargassum; in the Pacific's seal herds; in its salmon fauna with an oceanic phase, and in the kelp beds of its eastern margin.

These and other known differences make it highly probable that still others, perhaps more subtle and far-reaching, would be brought to light by adequate investigations, and so argue strongly for such investigations.

The paper is presented largely for the purpose of forwarding a plan already on foot for inaugurating the researches.

40. *Some notes with reference to infection with Sarcocystis tenella.* JOHN W. SCOTT, University of Wyoming.

Since the life history of this parasite is not known and since apparently 100 per cent of Wyoming range sheep are infected, the following notes will be of some interest. Lambs were kept in a dry lot from birth, and some were grazed with and without water being present. In all cases where lambs were grazed 100 per cent were infected. Some of the control lambs kept in the dry lot with pure water supply and fed on baled native hay cut the previous season, also became infected. Infection apparently does not take place in uteri, though the proof of this rests only on one definite case. Infection seems to occur only during the summer or early fall, not during the late fall, winter, or early spring. Proof of this rests upon results of the examination of lambs killed at different seasons. While sarcocysts vary greatly in size in lambs with identical treatment, the mean size gradually increases with age. However, the variation from an average mean size does not increase with age; hence an indication of early or summer infection. Another proof is that neither the percentage of lambs infected nor the amount of infection per cubic centimeter of muscle, increases during the winter. The amount of infection is very largely correlated with pasture conditions, and there is some proof that it is correlated with the presence of certain insects. Further discussion will appear in a paper soon to be published.

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PERSISTENCE OF THE POSTERIOR CARDINAL VEINS IN AN ADULT CAT¹

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ONE FIGURE

During the spring of 1917 one of the students in a class in vertebrate dissection reported a cat possessed of a double vena cava. This cat was then carefully dissected by the authors and an attempt is here made to explain the structures found as remnants of a condition carried through from embryonic stages to the adult form without further change. The cat was one picked up in the street, was very hardy and evidently had been foraging for itself for some time. Physically it was in fairly good condition with a moderate amount of fat around the kidneys. Its coat was in a filthy condition, but otherwise it was practically physically fit. The veins of the head, neck and thorax were also carefully dissected but they showed no great variation from those of a normal cat.

In the normal embryonic development of the cat the posterior cardinal veins run along the dorsal side of the mesonephros and enter the heart through the common cardinal veins. Each receives the internal iliac vein draining the posterior extremities, short branches from the mesonephros, and the segmental veins draining the body wall. The sub-cardinals are developed median and ventral to the mesonephros. These sub-cardinals are connected at intervals with the posterior cardinals by sinuoids, and with each other by anastomoses. Thus all of the blood from the mesonephroi and the posterior extremities is drained by the posterior cardinal veins alone during the early embryonic stages. Likewise in the cat here reported the per-

¹ Proceedings from the Zoological Laboratory of the North Dakota Agricultural College, No. 1.

sistent posterior cardinal veins drain the posterior limbs and the most of the blood from the now developed true kidney or metanephros.

The development of the unpaired vena cava inferior begins at the point where communication is established between the right hepatic vein of the liver and the right sub-cardinal vein, developed on the opposite side of the mesonephros and which is in reality a tributary of the post cardinal vein. A branch of the posterior cardinal vein encircles the ureter of the permanent kidney and is called the supra-cardinal vein. This has persisted in the adult cat on the left side. The permanent kidneys then take up their position opposite the large anastomoses between the posterior cardinal veins and sub-cardinals, and it is at this point that the renal veins are developed.

In the specimen found, there are two separate and distinct main veins running from each leg as far forward as the region of the kidney with absolutely no anastomoses along their course. The condition is clearly one of arrested embryonic development. These two main trunks can easily be identified as persistent posterior cardinal veins, having lost, however, the caudal anastomosis which is present in the embryo. The right side differs from the left in one particular only, and that is that the loop through which the ureter passes occurs on the left side only (fig. 1, C). This may easily be explained. Both ureters pass underneath the post cardinals, then curve sharply to meet the spermatic artery and vein (fig. 1, B). The ureter on the left side passes through a loop exactly as the ureter passes through a loop composed of the posterior and supra-cardinals in the embryo. Therefore, the median vein of this loop is without doubt the supra-cardinal vein. This vein receives the veins from the region of the spinal cord which would empty into the unpaired vena cava in the normal cat. This vein has entirely disappeared on the right side. It is readily seen, however, that the persistence of this vein is necessary on one side or the other in order that the region beneath the spinal cord be drained. As we go further forward the right sub-cardinal has united with the right hepatic vein of the liver and a single vena cava is pres-

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AUTHOR'S ABSTRACT OF THIS PAPER ISSUED BY
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MICROSCOPE LAMPS FOR STUDENTS

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College*

1. The following method will provide at very small cost microscope lamps which for ordinary student laboratories, are as satisfactory as the rather expensive lamps now on the market. 'Mazda' lamps of sixteen candle power with ground ('frosted') bulbs are dipped two or three times in a saturated solution of Bleu de Lyon in 50 per cent alcohol. After each dipping the lamp is permitted to dry. Wiring for the lamps is strung along the top of the table and protected by a metal strip one inch wide. Sockets are placed at the desired intervals. If students are seated on two sides of the tables, one such lamp will provide light for four persons. These lamps may be used effectively also for general illumination of the laboratories and offices.

2. Attention is called also to the new 'Mazda' lamps of higher power provided with a blue bulb, which are used commercially to illuminate show windows. These give a very strong nearly white light which is suitable for high-power microscopical work, but they are more expensive than the lamps described above.

CONCERNING THE RENAL PORTAL SYSTEM IN CHRYSEMYS MARGINATA

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TWO FIGURES

The presence of a renal portal system in reptiles is still an unsettled question. Whatever the significance of such a system, its presence has been definitely proven in fishes and amphibians, and its absence quite as surely shown in adult birds and mammals. But in the consideration of the question with respect to reptiles, one encounters contradictions, hazy statements, and lack of statement by various writers. The following table will indicate the position of authors on the subject:

AUTHOR	ARTICLE OR BOOK	DATE PUB- LISHED	STATEMENT
Owen.....	"Anatomy of Vertebrates"	1866	Hazy
Gegenbauer...	"Elements of Comparative Anatomy"	1878	Present in reptiles except Chelonia
Kingsley.....	"Vertebrate Zoology"	1899	Present in reptiles except Chelonia
Kingsley.....	"Comparative Anatomy of Vertebrates"	1912	Persists to a greater or less extent in adult reptile
Pratt.....	"Vertebrate Zoology"	1905	Present
Stromstem....	Anatomy and Development of Venous System of Chelonia. Am. J. Anat. 4: 453	1905	Belief of connections. No proof
Wiedersheim...	"Comparative Anatomy of Vertebrates"	1907	Only indications retained in adult
Wilder.....	"History of the Human Body"	1909	Not present in adult reptile
Agushi.....	Renal and suprarenal veins of Trionyx japonicus. Anat. Anz. 39, p. 183	1911	Capillaries in Trionyx japonicus
Hegner.....	"College Zoology."	1914	Absent in turtle
D. Lewis.....	"The Circulatory System of Chrysemys marginata" Thesis U. of Wis. (unpublished)	1916	Present in Ch. marg.

There seems to be a preponderance of statement among authorities that a renal portal system is not retained in reptiles, at least not in its entirety. We have Gegenbauer, Kingsley, and Hegner agreeing that there is none in turtles, and Wieder-sheim and Wilder that it is not present in the adult reptile; while opposed to these statements there is Pratt who says that the renal portal system is present in the turtle. As to original work on the problem, Stromstem believes that there are connections larger than capillaries between the posterior renal adve-hentes and the postcava in *Chelydra serpentina*, but he presented no evidence to prove it in his article. His work was general, including the anatomy and development of the entire venous system of several forms of *Chelonia*. The largest part of his work was on the hepatic portal system. Agushi in working on the Japanese form used the metal corrosion method with India ink injections and sections for a control. He claims to have demonstrated capillary connections, but his work is not conclusive. His work was not confined to the kidney but included the suprarenals as well. Dorothy Lewis in working out the general circulation of *Chrysemys marginata* was unable to get a starch mass into the postcava by injecting through the renal portal vein. She concluded from this that there were no connections larger than capillaries between them, and therefore that there was a true renal portal system in this form. The author tried several injections through the renal portal vein, none with success. The injection is difficult, and the results not at all conclusive.

This, then, is the status of the problem: the predominant note among writers on the subject seems to be that there is not a true renal portal system in the *Chelonia* at least, but there is no definite evidence to support this point of view nor is there any conclusive evidence given by those who hold that a renal portal system is present in the *Chelonia*. The need for specific work on the problem is evident. It is in the hope of giving some definite evidence that the author brings forward the results of his work on *Chrysemys marginata*. The attempt was, by means of a proper injection, suitable clearing of tissue, and careful

dissection, to demonstrate a connection larger than capillary between the renal portal vein and the postcava. Specimens of *Chrysemys marginata* were readily obtained from the lakes about Madison. In presenting the results of the work, the author wishes to thank Professor George Wagner for suggesting the problem and for other aid, and he desires to acknowledge to Mr. George Bishop not only many helpful suggestions but also time and effort spent by him in a large part of the injection work.

Before proceeding to the problem itself, it is advisable to give a brief description of the veins in the vicinity of the kidney of *Chrysemys marginata*. Running along the ventral side of the

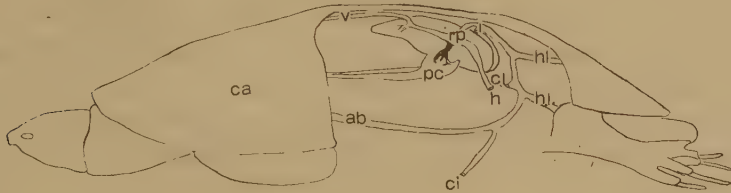


Fig. 1. Drawing of entire terrapin. *ca*, carapace; *v*, vertebral; *rp*, renal portal; *i*, stub of intercostal; *cl*, cloacal; *h*, hypogastric; *hl*, branches to hind limb; *ci*, common intercostal; *pc*, postcava; *ab*, right abdominal.

body between the plastron and the peritoneum are to be found the paired abdominal veins, extending from the region of the liver posteriorly to the sides of the pelvic girdle (fig. 1). In the latter position they pass dorsally and join the circumflex iliac veins. The circumflex iliac vein also receives the common intercostal vein from the lateral part of the carapace, veins from the hind limbs, and veins from the cloacal region. It is continued as the renal portal vein through a notch on the dorso-lateral edge of the kidney; and it divides into an anterior and a posterior branch on the lateral surface of the kidney. The anterior branch joins the vertebral vein, while the posterior forms the hypogastric draining the pelvic region. This differs from the description of Miss Lewis, for she says that the renal portal vein does not connect with the vertebral and that the

hypogastric is a branch of the circumflex iliac. The postcava is attached to the medio-ventral edge of each kidney, is unpaired, and forms a thin-walled sinus between the kidneys. The postcava runs anteriorly through the liver and opens into the sinus venosus.

Most of the time spent on the problem was used in discovering a proper manner of injecting and in experimenting with injection masses. It is not, therefore, out of place to review here the steps taken in developing a suitable technique and to give the results of the experimentation.

The first injection was done with a simple raw starch mass. Injections were made into the postcava, into the renal portal vein, and into the abdominal vein, each in a separate specimen. They were all made with a syringe. Injection into the postcava resulted in getting none of the mass through the kidney into the renal portal veins. In spite of this fact, connections larger than capillaries might exist between the veins, for valves might be present. The flow of blood is in the direction opposite to the injection, that is from the renal portal veins to the postcava.

Several injections were tried into the renal portal veins themselves, but without success. These veins are hard to find when uninjected, are short, and are easily injured.

Injections into the abdominal vein (preferably the left which is larger) resulted in finding the starch mass in the postcava. This indicated that there might be found a connection between the renal portal vein and the postcava.

This preliminary work with a starch mass was followed by double injections, gelatine mass followed by starch mass. And in this work of experimenting with various masses the following difficulties were encountered:

1. The thinness of the walls of the veins which were injected into made the work difficult and uncertain. The postcava though a comparatively large vessel was hard to inject on account of the delicacy of its walls. The renal portal veins presented this difficulty also. The abdominal veins are less

liable to injury, and yet some difficulty was found in getting an injection through them at times.

2. The testis or ovary is attached to the lateral surface of the kidney by means of a mesentery in which black pigment is deposited. This obscured the vessels on the lateral surface, and great difficulty was experienced in removing this mesentery without injuring the delicate walls of the veins beneath.

3. The question of the proper masses to show up the vessels to the best advantage was a problem. To bring out the vessels it was necessary to have a sharp contrast between the colors of the two masses used. A blue gelatine obscured everything in the kidney. The vessels injected with the starch mass must stand out against the kidney filled with the gelatine which goes into the finest capillaries.

After many trials the following two masses were used with good results. A cold gelatine mass was made up according to the Tandberg method as given in Guyer's "Animal Micrology" except that carmine was used for the pigment instead of Berlin blue. It was made up as follows: 5 grams of gelatine were added to 100 cc. of tepid distilled water. Carmine dissolved in ammonia was then added to the gelatine solution to give a light red color. Acetic acid was added to neutralize the ammonia, neutralization being indicated by the disappearance of the ammoniacal odor and the change in color to a bright red. 5 to 6 grams of potassium iodide were then added slowly, and finally a few crystals of thymol as a preservative. The mass remains liquid at ordinary temperatures, but solidifies when the object injected is placed in formaldehyde.

A starch mass was made up after experimentation in the following manner: 20 grams of starch were added to 550 cc. of water, and the starch cooked. 50 grams of Zinc oxide were added, and then enough 50 per cent potassium hydroxide to make the mixture smooth. A trace of soap was put in, and finally a few crystals of thymol to preserve. The starch mass cannot be preserved with formaldehyde, for such a mass following the cold gelatine sets the gelatine and interferes with the injection.

Successful injections with these masses gave a light red kidney against which the branches of the renal portal vein filled with the white starch mass, showed up clearly: It was found best to use an air pressure apparatus in the injection in place of the syringe, for it gave a steady pressure and filled up the smallest branches with the starch mass.

The injected terrapins were placed into 10 per cent formaldehyde to set the gelatine and then into 50 per cent alcohol to set the starch. The kidneys were dissected out and placed into 95 per cent alcohol. They were then cleared by running them through absolute alcohol, then benzol, and finally a mixture of oil of wintergreen and isosafrol (oil of wintergreen 5 parts and



Fig. 2. Terrapin A, right kidney. *rp*, renal portal; *v*, vertebral; *pc*, postcava; *h*, hypogastric.

isosafrol 3 parts) following the Spalteholz method for clearing. One kidney was then drawn entire to show the distribution of the blood vessels, and then thick sections were cut, arranged in series, and drawn to show the vessels in the kidney injected with starch.

In two series of kidney sections indication was found that a connection larger than capillary existed between the renal portal and the postcava. In sections about midway between the anterior and the posterior ends the starch mass was found extending from the region of the renal portal to the postcava. For verification a number of kidneys were dissected on the lateral surface to demonstrate the connection. Two dissections were successful. A right kidney is shown (fig. 2) with the vessel extending down from the renal portal to the postcava.

It was found by dissecting off carefully the entire mesentery of the ovary or testis. A similar connection is clearly seen also in the drawing of the entire terrapin (fig. 1).

These results show a connection between the renal portal vein and the postcava, a connection larger than capillary. While there may be capillaries present also between the two veins, yet the demonstration of a larger connection proves at least that the renal portal system is not complete.

CONCLUSIONS

The following results were obtained in this work on *Chrysemys marginata*:

1. Injection of a starch mass into the postcava resulted in finding none in the renal portal vein. This does not disprove a connection larger than capillary, for valves might be present.

2. Injection of starch into the renal portal vein was unsuccessful.

3. Injection of starch into an abdominal vein resulted in finding the mass in the postcava.

4. By means of a double injection a connection was demonstrated between the renal portal vein and the postcava. This proves at least that a complete renal portal system does not exist in *Chrysemys marginati*.

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OBSERVATIONS ON THE SHAPE OF THE ERYTHRO- PLASTID IN THE WING OF THE BAT

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In previous publications ('16, '17) there has been presented in detail the evidence derived from the study of drawn blood, circulating blood, and fixed preparations which has led the writer to conclude, contrary to certain recent investigations, that the biconcave disc represents the normal shape of the mammalian erythroplastid—the concavo-convex 'cup' being merely an occasional constituent of the blood.

For reasons that are obvious the inspection of blood circulating in the transparent parts of mammals should furnish reliable information upon this topic. There are, nevertheless, certain sources of error to be avoided: only vessels of greater calibre than a red corpuscle are suitable for study; the effect of pressure upon small vessels must be eliminated or controlled; the possible influence of the anesthetizing agent carried in the plasma upon the circulating corpuscles (similar to its demonstrable effect in modifying the shape of drawn corpuscles) must be shown not to exist or else non-anesthetized animals used.

In the studies upon circulating blood, the omentum and mesentery have largely been employed. It is hardly reasonable to urge that the necessary exposure of these parts during the examination, inviting though it does drying, stasis, and inflammation, need militate against the validity of the results, yet if these abnormal conditions can be avoided a valuable check is thereby gained. The only situation which might appear a priori to be more favorable than the omentum or mesentery is such an one as is furnished by the wing of the bat. In the present communication it is proposed to present evidence derived from this source.

¹ Contribution No. 51, October 1, 1917.

Since an extended review of the literature has been published recently by the writer ('17) only those contributions bearing directly upon the subject at hand need be mentioned.

Weidenreich ('03) recommended for study the wing of the hibernating bat, evidently intending to infer that cup-shaped corpuscles would be found.

Jolly ('05) also reported observations upon the bat's wing². He asserts that rouleaux occur normally in the capillary circulation, these breaking into short segments which persist in the veins, only to reform long rows if the current slackens; in support of this claim a similar finding by Weber and Souhard ('80) on curarized dogs is cited. In rouleaux he found the separating lines to be transverse, the terminal corpuscles of short trunks discoid, while corpuscles free in the plasma likewise had the disc configuration. Exceptionally cup shapes were seen at the end of rouleaux or free.

Weidenreich ('05) denied that rouleaux exist in the normal circulation and suggested that Jolly must have observed capillaries in which the flow had almost or wholly ceased. He adds that in the bat's wing he has repeatedly seen only cups. Again in 1906 Weidenreich reiterates these points, objecting that Jolly saw corpuscles compressed into rouleaux by incipient stasis, whence their true form vanishes; *cc . . . da ich wiederholt schönste Napfformen und zwar nur Napfformen sah, besteht für mich kein Grund von meiner Deutung abzugehen.*"

Jolly ('06 a) denied that stasis influenced his results and this and later publications ('06 b; '09) simply re-emphasize his former contentions.

My own observations have been made during the preceding summer upon a number of bats³ of two species.⁴ The animals

² From a footnote in a later communication ('09) it appears that many of the animals used in his experiments were prematurely aroused from hibernation; this he believes neither involves complications nor introduces a source of error.

³ For the procural of these animals I am indebted to the persistent efforts of Mr. J. R. Reuling of Muscatine, Iowa.

⁴ *Lasionycteris noctivagans* Le Conte: *Vespertilio gryphus lucifugus* Le Conte.

were held by an assistant⁵ and the wing spread on a glass plate over the microscope stage; various lens combinations were employed both with and without the aid of a cover glass.

The keratinized and pigmented epidermal cells make observation less simple than in the inspection of a mesentery. Nevertheless a thorough search usually reveals a favorable location, and experience soon enables one to overcome surprisingly the early observational difficulties. Small vessels branching off from larger ones in a recurrent manner often afford a favorable site. Minute capillaries merely large enough to allow corpuscles to pass in single file are to be avoided for here crowding and distortion are inevitable; stretching of the wing also flattens small vessels by increasing their lateral diameter, whence corpuscles pass through more or less on the flat thereby producing a deceptive picture of innumerable cups (*vide infra*).

It is often possible to control the blood flow by applying pressure of the finger to large vessels in more remote regions of the wing; such manipulation may induce a rhythmical flow of a halting or pulsating nature, whereby individual corpuscles can easily be watched and made to revolve; in other instances corpuscles pass by continuously, a few at a time. The normal circulation, with a minimum of interference, was, however, given the preponderance of attention.

I do not believe that the occurrence of rouleaux within the normal circulation, as maintained by Jolly, is in accord with the facts. When corpuscles pass under pressure in single file through capillaries, temporary piles of approximated elements undoubtedly form. In varying abundance they may also be found in larger vessels, but I feel confident that this is correlated with some artificial restriction to the usual flow; I hold it probable that this condition can be induced or aggravated by inhibiting the current distad of the spot under inspection. It is significant that Jolly neither describes nor figures rouleaux in the

⁵ It is a pleasure to acknowledge the valuable assistance rendered by Mr. F. H. Reuling during the course of these experiments. In several instances he has checked my observations and with identical results.

arterial circulation where he states ('09, p. 101) “. . . la rapidité du courant empêche de distinguer nettement les globules.” The explanation of Jolly's contention may exist in the circumstance that many (or most?) of his experimental animals had been recently in their dormant winter state where the circulatory condition is presumably that of *essentia* stasis.

Eliminating the deceptive simulations of cups afforded by corpuscles viewed obliquely on the flat,⁶ I was able to convince myself of the normality of the disc shape. I do not believe that, in the bat at least, an opinion concerning the shape of a corpuscle carries weight unless that particular corpuscle is seen on both faces, or at least in perfect profile. Blood drawn from a cut between two opposed cover glasses, fused at one point and separated by a hair, confirmed this opinion; many corpuscles were seen which appeared as veritable cups until rotation presented an edge view. This illusion I do not remember having seen so strikingly before in the blood of other mammals (cf. '17, p. 469); the impression was gained that in these corpuscles the excavated faces were especially deep, this perhaps being due to thicker rims.

The foregoing observations on the wing of the living bat support the contention that the mammalian erythroplastid is correctly described as a biconcave disc.

⁶ David ('08) and Löhner ('10) have emphasized the importance of this illusion and have constructed elaborate models to demonstrate its actuality.

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A SEASONAL STUDY OF THE KIDNEY OF THE FIVE-
SPINED STICKLEBACK, EUCALIA INCONSTANS
CAYUGA JORDAN

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TEN FIGURES

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INTRODUCTION

It is a matter of general knowledge among Zoologists that the sticklebacks, family Gasterasteidae, constitute a group of fishes in which the nest-building instinct is very pronounced. The nest varies with the species since that of the five-spined stickleback (text fig. 1) is constructed largely of algae and other small water plants, while certain of the larger marine species build their nest chiefly by drawing together the vegetation close at hand, though sometimes leaves and other débris, found in the water, are used. This material is shaped into form by the male, and fastened together by means of a substance secreted by the kidneys. The secretion has been mentioned by many authors as silk, and is described and figured in connection with

several species, as slender, thread-like strands similar in appearance to spider's silk.

The present study was undertaken with a view to demonstrating what portion of the urinary tract functions in this



Text fig. 1 A drawing of a nest of the fine-spined stickleback, *Eucalia inconstans cayuga* Jordan. Drawn from photographs by Dr. E. E. Barker, and a nest in the collection of the Zoological laboratory.

process, what changes the various cells undergo at different seasons of the year, and finally to determine if possible the nature and kinds of secretions.

The writer is sincerely indebted to Dr. H. D. Reed for suggestions and criticisms throughout the progress of this work; also to Dr. R. J. Gilmore for material which he kindly donated.

MATERIALS AND METHODS

Material for this work was collected monthly throughout the year, except for about two months during the middle of winter. Since previous workers disagree as to whether the females function in producing the secretion, both males and females were preserved for study. The majority of the fishes were killed in the fixing fluids with the abdominal cavity opened. The kidneys of several were removed and preserved separately.

The chief fixers used were: Zenker's fluid; mercuric chloride; 10 per cent formalin; Flemming's (strong formula); Benda's; and Zenker's fluid with the acetic acid used in the proportion of one drop to ten cubic centimeters.

In order to determine the seasonal changes in the kidneys, serial sections, varying in thickness from three to ten microns, were made of the kidneys of both males and females, taken at the different seasons.

For general staining, Delafield's haematoxylin and eosin were very satisfactory. For more detailed study those killed in Flemming's solution, and stained in Heidenhain's iron haematoxylin proved most satisfactory, though eosin was often used as a counter-stain. Flemming's triple stain was used but with little success. Ehrlich's triple stain proved very satisfactory in showing secretion granules after fixation with Zenker's fluid.

For cytoplasmic structures, and to clearly differentiate certain protozoan parasites present, copper haematoxylin proved an excellent stain after fixation with Zenker's fluid in which the acetic acid was used in the proportion of one drop to ten cubic centimeters.

In order to demonstrate the portions of the kidney which form the secretion, a wax model, as a reference aid, was constructed from serial sections of the kidney of a male taken at the end of the active period.

HISTORY

Though many observations have been made on the biology of this peculiar group of fishes, no extensive observations have been made on the histology of the organs, which form the secretion used in constructing the nest.

As early as 1828, according to Möbius ('85), David Milne observed the ten-spined stickleback (*Spinachia vulgaris* Flem.), building its nest at the breeding season. Since that time many authors have reported similar observations.

Coste ('48) described in detail the building of the nest by the sticklebacks. He found that the material of the nest was shaped into position by the fish, and thought that the intensive rubbing of the fish's body against this material caused it to remain in position in the nest. He does not seem to have discovered the secretion.

Couch ('65) described the method by which the fifteen-spined stickleback builds its nest. He found that the fish secreted a material in the form of a thread which was used in binding the material of the nest together. This thread resembled silk, was elastic, and under magnification, appeared to be composed of several smaller threads glued together. Though he does not directly maintain that he traced the origin of the secretion, he states that there is no doubt but that the substance is obtained from the animal's own body.

Ranson ('65) described very interestingly the biology of the ten-spined stickleback (*Gasterosteus pungitius*). He showed that the male alone constructs the nest in which he then actually forces a successive number of females to deposit eggs. He seems to have overlooked the secretion entirely, for he refers to the building of the nest as an interlacing of fibers of small water plants.

Heincke ('82) was apparently the first to discover the true source of the secretion; namely, the kidneys. He maintained that the male and female together constructed the nest, and stated that the secretion, as it passed from the fish, was in the form of a white slimy thread.

Prince ('85) described the thread-like material which binds the nest together, as a colorless, tenacious substance, of the consistency of mucilage when fresh. It exhibits a delicate blue opalescence, which disappears in two or three days, leaving the threads of a transparent gray or a soiled-white color.

Möbius ('85) first definitely pointed out by histological study that the kidneys of the male stickleback produced the secretion for constructing the nest at the breeding season. He claimed to have found two kinds of secretion, which he designated respectively as mucigen and mucous. Most of the epithelial cells secreted the mucigen as a thread-like material, the finer strands of which were formed in the coiled kidney tubules, the coarser ones in the collecting tubules. The mucous-secreting cells were found interspersed between the other kidney cells. Their nuclei disappeared during the process of mucous secretion, while the nuclei of the mucigen forming cells became flattened and ridged. Following this period of active secretion the mucous secreting cells became slender, and the nuclei passed into the lumen with the last of the mucous substance.

Möbius did not say whether the urinary ducts function in forming the secretion, but he stated that the bladder took no part in this process.

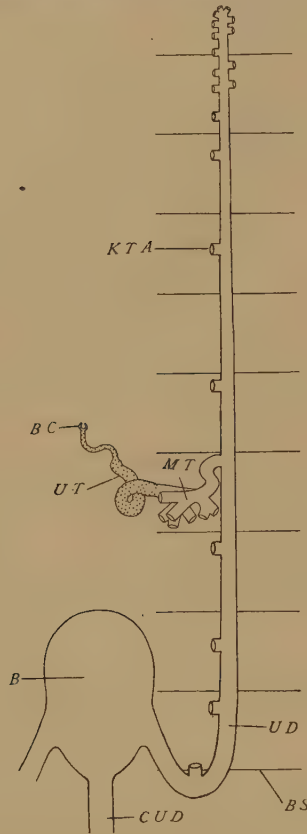
Like Couch ('65), Möbius described the thread as composed of a mass of smaller threads glued together.

GENERAL MORPHOLOGY OF THE STICKLEBACK KIDNEY

Since it has been claimed by certain authors that both the male and female fishes construct the nest, sections of both sexes were cut at different periods during the breeding season. It was readily seen that only the male forms the secretion, for the kidneys of the female showed no signs of the special glandular activity so characteristic of the male at this period.

Möbius ('85), in his work on the sticklebacks, maintained that the entire kidney functions in producing the secretion, but since the histological preparations showed distinctly that only a portion of the kidney was functional in this respect, a wax model was constructed, from drawings of serial sections, in order

to demonstrate what portions were involved. In making sections for this purpose, fish were taken at the end of the breeding



Text fig. 2 A diagrammatic drawing, made from a model of the nephridial tubules of a male stickleback at the breeding season, showing the regions which form the different secretions. The portion shown in stipple secretes urine. The unshaded portions produce the slime-like secretion. *B*, bladder; *BC*, Bowman's capsule; *BS*, body segment; *CUD*, common urinary duct; *UT*, uriniparous tubule; *KTA*, kidney tube attachment; *MT*, muciparous tubule; *UD*, urinary duct.

season when the cells, specialized for forming this secretion, were entirely vacuolated.

Text figure 2 is a drawing of the model referred to above. No attempt was made to show the kidney tubules of the dif-

ferent segments, except in one, where an entire kidney tubule is represented. It will be seen that the tubule consists of eight branches which unite a short distance from the urinary duct to form a single tubule. The tubule, shown in stipple with a Bowman's capsule at its end, consists of columnar epithelium and is subservient to the usual excretory function. Those portions of the tubules which are urinary in function, the writer has designated as the uriniparous tubules (*UT*), while the portions which secrete slime form the muciparous tubules (*MT*).

The uriniparous tubules are of about the same diameter as the muciparous tubules for a short distance when they suddenly become constricted and much coiled. Unlike the muciparous tubules, they were never found branched. At the end of each uriniparous tubule is a Bowman's capsule.

The portions of the kidney which secrete the slime are termed the muciparous tubules, the urinary ducts, the bladder and the common urinary duct. At the height of the slime secreting period the epithelial cells of all these regions are vacuolated throughout their entire extent.

In the remaining body segments only the kidney tubule attachments are shown, since the general condition of each is the same as the one figured.

The caudal three-fourths of the kidney has, as a rule, only one set of tubules attaching to the urinary duct in each segment, though one segment was found in which no tubule was present. On the other hand, towards the cephalic end of the kidney the tubules were very numerous. Here, together with the lymphatic tissue so characteristic of the anterior part of the fish kidney, they cause a conspicuous enlargement.

Following the breeding season, the kidneys of the male are of about the same volume as those of the female. This condition lasts until late in January or February, when those of the male again increase in size preparatory to glandular activity.

It seems rather peculiar that the first signs of glandular activity in the early spring occur in the distal ends of the muciparous tubules. These become functional before there appears to be any evidence of activity elsewhere. Though it seems

probable that all the muciparous tubules become active about the same time, the earliest signs of activity appeared to be in the cephalic region of the kidneys. From the appearance of the cells at different periods during activity, it is clearly evident that there is a difference in the amount of secretion produced in different regions. The cells of the muciparous tubules become active first and secrete the greatest amount of slime. The cells of the urinary duct anterior to the bladder, next, then those of the bladder, and finally those of the common urinary duct, whose cells seemingly secrete the least of all.

Thus it is obvious, that the male only produces the secretion, and that the epithelium of the muciparous tubules, urinary ducts, bladder and common urinary duct are active in producing the special secretion. The bladder is especially large in this species, and serves as a reservoir for the secretion, as well as contributing to its production.

HISTOLOGICAL STRUCTURE OF THE DIFFERENT KIDNEY CELLS DURING THE RESTING, OR WINTER STAGE

From the first of July until the following February, the cells of the kidney show no signs of activity other than that of ordinary kidney cells, and hence this period can be spoken of as the resting stage as regards slime secretion.

The cells of the muciparous tubules during the month of December (fig. 1) appear considerably different from those of the uriniparous tubules (fig. 2), though less differentiated than at the breeding season. The nuclei are nearly round, containing one large nucleolus, and a fine network of chromatin. The cytoplasm is of a fine granular character, though somewhat irregularly grouped, which appearance, however, may be due to fixation. The cells are very similar in histological structure to those of the urinary ducts (fig. 3), except that they are not as large and less columnar. The cells of the bladder and common urinary duct are similar to those of the urinary ducts.

The condition of the uriniparous tubules, at this season, is rather peculiar, in that the nuclei are very much enlarged, though the cells themselves are smaller (fig. 2) than during the

spring (fig. 7). At this time, as at other seasons, these nuclei usually possess two large nucleoli about which can be seen an irregular chromatin network.

No attempt was made to study the cells of the smaller portion of the uriniparous tubule, other than to note that at this season, and also in the spring, they resembled the other uriniparous tubule cells, except that they are smaller and less columnar. It cannot be stated that the cells of the male and female kidneys at this stage are alike histologically. In the female all the cells of the kidney are of a similar histological structure, there being no difference between the cells of the different regions, such as has been described above for the male.

HISTOLOGICAL STRUCTURE OF THE DIFFERENT KIDNEY CELLS AT THE BREEDING SEASON

In the region of central New York, about the first of February the cells of the muciparous tubules, urinary ducts, bladder and common urinary duct of the male stickleback first begin to show signs of activity. The cytoplasm stains lighter in these cells than in those of the uriniparous tubules, while their nuclei stain slightly darker, due to a rather denser granular content.

About the middle of February, the cells of the proximal kidney tubules begin to secrete the slime. By the first to the middle of March, all the other portions, including the urinary ducts, bladder, and common urinary duct become functional. Schiefferdecker ('84) found a somewhat similar condition in the bladder of *Rana esculenta* and *Bufo vulgaris* during the breeding season. Heidenhain ('90) working on the Tritons, found a similar condition in the cloacal region at this period.

Among the first signs of glandular activity is the appearance, between the nuclei and the ends of the cells next to the lumen, of rather large granules, called here, secretion granules. Granules somewhat similar in appearance may be seen within the nuclei. The nuclei, however, at this stage appear very similar to their earlier condition.

Maziarski ('11) in a study of the silk glands of lepidopterous larvae, states that the nucleoli migrate out into the cell body

where they participate directly in the formation of the secretion. Nakahara ('17) claims that in the silk glands of certain insects, portions of the nucleoli migrate into the cell body and form, at least, a part of the secretion products of the cell. While the kidney cells in the stickleback are much different from those that secrete silk in insects, there is, however, some similarity in the methods of secretion.

Garnier ('00) from a study of the salivary gland of the rat, and Maxinow ('01) working on the same gland of the dog, claim that the migrated 'nucleolekörper' are metabolized into secretion products. On the contrary, Carlier ('99, '05) working on the stomach and liver cells of the newt, opposes the view that the nucleolar material can be considered as playing a rôle in the formation of the secretion substance. He maintains that the nuclei give up prezymogen, which is produced from chromatin, that this is changed to zymogen in the cytoplasm, and finally into the secretion.

Another observation important in this connection is the more recent view of glandular secretion upheld by Arnold ('05), Hoven ('10, '11) and Schultze ('11), which has grown out of the discovery of mitochondria or chondrisomes, widely distributed in the cytoplasm of glandular cells, and supposed to give rise to the secretion granules.

Of the three views, the last seems the least probable in the case of slime secretion in the stickleback-kidney. The delicate fixers and stains to distinguish mitochondria were used, but in no instance was there any evidence that such was the source of the secretion granules. On the other hand, the writer was unable to find the nucleoli dividing, or to observe the secretion products passing out of the nucleus. As the process of secretion progresses the nuclei appear to cave in on the side toward the free ends of the cells, indicating that the nuclear substance is diminished. The nucleoli in these cells are rather small at all stages, unlike the condition of true silk gland cells. It is possible that these nucleoli function directly in producing the secretion granules but it seems more plausible that certain products of the karyoplasm pass into the cytoplasm forming the secretion

granules. Whatever may be the origin of these granules they appear to function in breaking down the granular cytoplasm of the cell, thus forming the secretion.

As the cell becomes active the granular protoplasm in the center of the cell, in a direct path between the nucleus and the free margin of the cell breaks down giving rise to the slime (fig. 4 A). In this region the cells begin to appear vacuolated. This vacuolated area gradually enlarges until it occupies practically the entire area between the nucleus and the free end of the cell. The secretion granules appear to be rather evenly arranged, usually lying near the center of the cytoplasmic vacuoles where these have appeared.

As the distal part of the cell becomes well vacuolated, due to the continued formation of the secretion, the side of the nucleus towards the free end of the cell seems to cave in toward the base of the cell (fig. 4 B). Secretion granules continue to be formed but not as rapidly as in earlier stages. The nucleus, as shown in the figures, migrates to the base of the cell, where it becomes more and more flattened, until finally it lies at the base of the cell as a flat dark-staining irregular mass (fig. 4 C). While this is taking place the granular protoplasm at the base of the cell is being gradually broken down, until finally the entire granular protoplasm of the cell has disappeared (fig. 6).

Even after the granular protoplasm has disappeared, the cell vacuoles often remained full of secretion for some time (fig. 5) and take a deep blue stain with Delafield's haematoxylin. As the last of the secretion passes into the lumen of the kidney tubule, the cell becomes a non-staining vacuolated structure except for the small shrunken nucleus and the network of the vacuoles (fig. 6).

Since the muciparous tubules are the first to become active, it is only natural that they should first become exhausted in forming the secretion. As the cells become active and produce secretion they have a tendency to become broader and shorter than earlier in the season.

The transition, between the slime secreting portions of the kidney tubules and the urinary portions, is rather abrupt, as

is shown in figure 7. The slime secreting cells are broad and rather flat, while those urinary in function are long and slender. Since this preparation, shown in figure 7, was made towards the end of the active season, the slime cells contain little or no secretion. As can be readily seen, the nuclei of the urinary cells adjacent to those producing slime, are relatively small. These cells and their nuclei, however, increase gradually in size until at about the third cell from the last muciparous cell they assume the characteristic appearance of the normal urinary cells.

Normal urinary cells at this season of the year show no marked changes. The nuclei are nearly round, and lie a short distance from the base of the cells. They may contain one, two or three nucleoli, but usually two, while the cells of the slime secreting type were never found with more than one nucleolus. The cytoplasm of these cells was very granular and irregularly grouped.

With such fixing fluids as Flemming's (strong formula) or one per cent osmic acid, and with Heidenhain's iron haematoxylin staining, the urinary cells were found to contain rather large granules, resembling those of the slime secreting cells. Some of the cells seemed to take up more of the osmic acid than others, and hence appeared dark and structureless. Möbius ('85) described these cells as forming a second kind of secretion. By destaining, however, they were found to be ordinary urinary cells. All of these cells were pouring into the lumen of the tubule, a substance which appeared to be an irregular granular mass. After a careful study of the kidneys of this and other species of fishes, the author is convinced that these are normal urinary secreting cells.

NATURE OF THE EXUDED SECRETION

Since it is often difficult to judge the nature of a secretion from its histological structure before being exuded, the structure of the substance after it has been used by the fish in constructing its nest will be considered briefly. Couch ('62), Möbius ('85), and Prince ('85), working on European forms, each described the structure of the material as being composed of threads

resembling silk. The threads were elastic and under a microscope appeared to be composed of several smaller threads glued together. Heincke ('82), on the contrary, referred to the secretion as consisting of a white slime-like substance. The writer's observations on the nature of this secretion confirms the work of Heincke, since no evidence of a fibrillated nature was to be distinguished, even with a high magnification. The fish often deposits the secretion in ribbon-like masses as may be seen in among the plant substance of the nest (text fig. 1). This secretion, upon histological examination, appears to consist of a very fine granular slime-like substance. It may function somewhat as a string in binding the material of the nest together, but probably is more in the nature of an adhesive substance.

REGENERATION OF THE GRANULAR CYTOPLASM WITHIN THE SLIME-SECRETING CELLS

The process of secretion which reaches its maximum early in April continues late into May, and sometimes to a very slight extent into June.

Early in June there takes place within the slime secreting cells, a process whereby the granular cytoplasm is again restored so that the cells present an appearance similar to that of the cells before the secretion began to be formed. Schiefferdecker ('84), working on the sublingual glands of the dog, found that new gland cells are formed at the base of the secreting cells, and gradually the old vacuolated cells were sloughed off. There is no evidence of any such process in the sticklebacks. Heidenhain ('90), in his work on the cloacal glands of the Triton, maintained that the protoplasmic granules regenerate themselves. This, in the kidney cells of the stickleback, seems impossible since at the end of secretory activity all the protoplasmic granules have disappeared. Moreover, at the time of regeneration, the granules are not uniformly distributed throughout the cell, but always found about the nucleus.

The first change observed in the regeneration of these kidney cells was an enlargement and rounding of the nucleus. At the same time, in fact, as soon as the nucleus began to show signs

of activity, there were observed inside the nucleus, numerous acid staining granules. In the body of the cell the cytoplasmic granules appeared first at the base, around the nucleus, and gradually came to occupy the entire cell. In most cells, as these granules began to be formed, the nucleus migrated some distance towards the middle of the cell. In every case the cytoplasmic granules were most numerous about the nucleus during their early stages of regeneration.

Since the granules first form about the nucleus it seems that the nucleus must be discharging certain substances into the cytoplasm, which act upon the protoplasm of the cell restoring the granular condition. It does not seem probable, however, that these granules are formed within the nucleus and discharged into the cytoplasm. At any rate, it seems that the nucleus must play an important part in this regeneration. If these cytoplasmic granules are the products of mitochondria or similar cytoplasmic components, why do they form just around the nucleus and not evenly, or at least scattered, throughout the cell?

COMPARISONS WITH THE KIDNEYS OF OTHER FISHES

In order to obtain a more definite idea of the typical fish kidney, sections were made at the breeding season of the kidneys of the male bullhead (*Ameiurus nebulosus* LeSueur), the black-nosed dace (*Rhinichthys atronasmus* Mitchill), and the gold fish (*Carassius auratus* L.). It was readily seen that no special secretion of any kind was formed by their kidneys, and that the cells of the kidney tubules, urinary ducts, bladder and common urinary duct resembled in general those of the female stickleback. The cells of certain tubules in the gold fish kidney were found to contain cytoplasmic granules only at their lumen end, in which region was found a rather shrunken, often irregularly-shaped nucleus. The basal portion of the cells appeared as large clear areas. In some cells the granular cytoplasm appeared to be practically absent, and the nucleus was very much reduced. The exact significance of this condition is doubtful. It may represent a degeneration. This particular

fish had been kept in the laboratory under artificial conditions for about a year, and it is possible that this would account for the above described condition. The other kidney tubules appeared normal.

KIDNEY PARASITES

The habits of these little fishes are very peculiar and no doubt are conducive to parasitic infestation. The writer has found them living in various places, and under varying conditions, but usually in shallow, slowly flowing water in which plants are abundant. Some were collected in pools which were so nearly dry that they consisted of a rather blackish muck, from which other species had disappeared, while these were apparently inconvenienced in no way. They were found abundant in meadow streams in among the water plants, in swamps and among the water plants along the shores of Lake Cayuga, New York.

Nearly all specimens collected showed, upon histological examination, an abnormal condition of the kidneys. Scattered among the cells of the various tubules and ducts of the kidneys of both male and female at all seasons of the year, were found numerous protozoan parasites. No attempt was made to study their life history. When mature the spores and finally the body of the old parasite, are discharged into the lumen of the kidney tubules.

What apparently is the same organism was described by Thelohan ('92) as a *Coccidia*n. He found the parasite widely distributed among fishes, and in various tissues.

Though black-nosed dace were taken in the same places as the sticklebacks, which possessed the kidney parasites, these fish showed no signs of any such infestation.

SUMMARY AND CONCLUSION

The secretion, by means of which the five-spined stickleback builds its nest is produced by the male alone, and only at the breeding season.

During the greater part of the year, the male kidney is an excretory organ. At the breeding season, however, only what

we term here the uriniparous tubules and glomeruli function thus, while the cells of the muciparous tubules, urinary ducts, bladder, and common urinary duct become modified for the purpose of producing slime.

In the process of slime secretion, the behavior of the nuclei is such, that they evidently pour into the cell bodies certain products, in the form of secretion granules, which function in breaking down the granular cytoplasm of the cells, and thus form the secretion. These secretion granules appear to be produced from certain products of the karyoplasm, as this substance gradually diminishes in amount during this process. It is possible that the nucleolus functions in this process.

Only one kind of secretion is produced for constructing the nest. This material is not silk, nor is it composed of fine fibrils, but appears as a fine granular slime-like substance. It is sometimes exuded in ribbon-like masses, but it probably functions more as an adhesive substance, than as a string, in binding the material of the nest together.

The exact process by means of which the cytoplasmic granules are regenerated, following the process of slime secretion, is uncertain, but it seems evident that the nucleus is the active agent.

During the resting or winter stage, the cells which form the slime during the spring appear much like those of the uriniparous tubules, except that their nuclei are smaller. At this season the nuclei of the uriniparous tubule cells are very large, often occupying at least half of the cell contents. The investigation justifies the conclusion that the whole kidney is not transformed periodically into a silk or slime producing gland as one is led to infer from other published accounts but that the process of slime secretion is due to the activity of the epithelial cells of various ducts and tubes of the system not engaged in the excretory function. It is comparable to the secretion of slime by the genital ducts of Amphibia during the breeding season.

From a comparison with fishes of diverse habits and affinities, it would seem that the formation of this slime secretion by the kidneys of the sticklebacks is probably unique among fresh water forms.

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PLATES

PLATE 1

EXPLANATION OF FIGURES

- 1 Cells of the muciparous tubules, taken December 8. (*N*), nucleus.
- 2 Cells of the uriniparous tubules, taken December 8. (*N*), nucleus.
- 3 Cells of the urinary duct, taken December 8. (*GC*), granular cytoplasm; (*N*), nucleus.
- 4 Cells of a proximal collecting tubule showing different stages in the early process of secretion.

Cell A, a rather early stage of cellular secretion. Between the nucleus (*N*) and the free end of the cell the normal cytoplasmic granules are disappearing. Scattered about in the cytoplasm are many secretion granules (*SG*). At the base of the cell the normal cytoplasmic granules are unmodified.

Cell B, a little more advanced stage of secretion than *cell A*. The nucleus (*N*) appears as if fallen in on the side towards the free end of the cell. Secretion granules (*SG*) are abundant. The vacuoles (*V*) so characteristic of later stages are becoming prominent.

Cell C, a rather late stage in the process of secretion. The nucleus (*N*) is very much flattened and shows a tendency to wander towards the base of the cell. The vacuoles (*V*) are very prominent though at this stage they are full of secretion. Fish taken February 16.

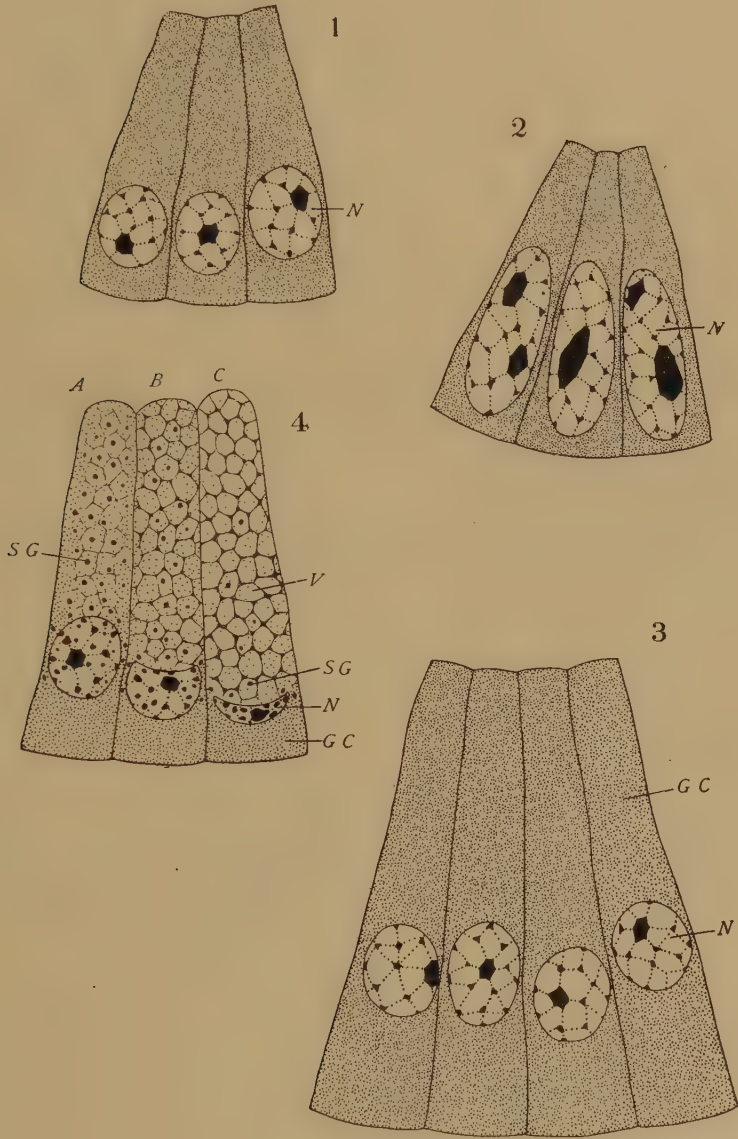


PLATE 2

EXPLANATION OF FIGURES

5 Cells filled with secretion, the nuclei (*N*) have wandered to the base of the cells. The normal cytoplasmic granules have disappeared. The vacuoles (*V*), filled with secretion, are very prominent. Fish taken April 1.

6 Cells at the end of the secreting period. The vacuoles now appear empty of secretion. There is no evidence of the normal cytoplasmic granules. Fish taken May 1.

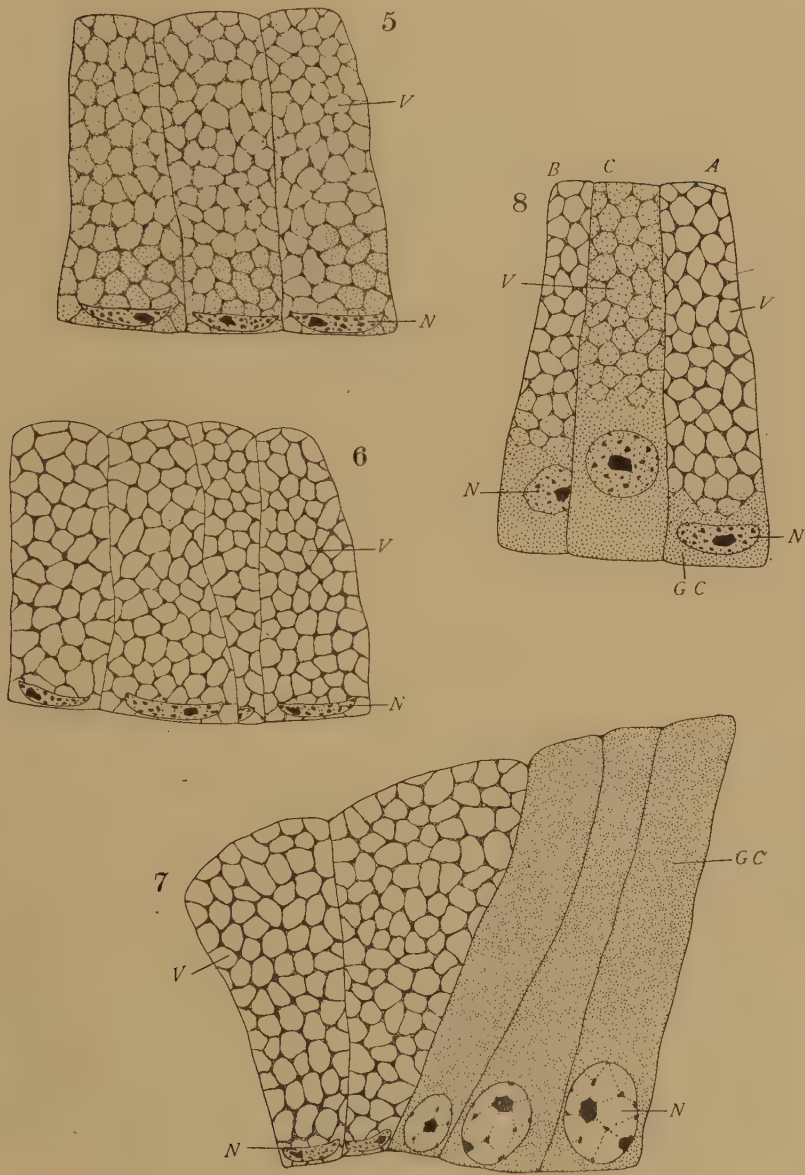
7 A few cells to illustrate the transition between the proximal collecting tubules and distal collecting tubules at the end of the active period. The distal collecting tubules contain granular cytoplasm (*GC*), while those of the proximal collecting tubules are vacuolated (*V*). Fish taken May 1.

8 Cells of the urinary duct to illustrate stages in the regeneration of the granular cytoplasm (*GC*) after the breeding season.

Cell A, shows the nucleus in the early stage of activity. Cytoplasmic granules are forming about the nucleus at the base of the cell. The nucleus is wandering towards the center of the cell. Vacuoles are now indistinct where protoplasmic granules have formed.

Cell B, a more advanced stage than *Cell A*. The nucleus (*N*) has enlarged and wandered farther towards the center of the cell. Cytoplasmic granules are increasing.

Cell C, cytoplasmic granules now nearly fill the cell. The nucleus (*N*) appears nearly normal. The vacuolation is rapidly disappearing. Fish taken June 20.



HISTOLOGY OF THE SENSORY ROOT OF THE TRIGEMINAL NERVE OF THE RAT (*MUS NORVEGICUS*)¹

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During the course of a general study of the structure of medullated nerve fibers, a Weigert stained longitudinal section of the sensory root of the trigeminal nerve from a wild rat (*Mus norvegicus*) was examined. It presented, about 1 mm. from the brain stem, a sharply defined line of transition between the structure of the peripheral nerve trunk and the central nervous tissue, which change was revealed particularly by a difference in the intensity of staining. This change occurred along a regularly curved transverse line which was slightly convex peripheralward. A cursory examination of similarly prepared sections from the same and other animals showed that this condition was normal and not an artifact.

This picture has been described by a number of observers, more from the standpoint of microscopic relations than from the detailed histologic standpoint. A brief review of the most important communications will be both valuable and interesting.

R. Thomsen ('87) observed, in cross-sections of the human abducens and oculomotor nerves from a case of multiple alcoholic neuritis, that there were small, round, glistening plaques or 'Herde' lying in the normal nerve tissue of the trunk and sharply delimited from it. They consisted of a horny substance staining readily in carmine. Oppenheim ('87) found similar plaques in cross-sections of the human facial and hypoglossal nerves and designated them as the 'Herde' of Thomsen. The latter, having recognized that these 'Herde' were not specific

¹ In partial fulfillment of the requirements for the degree of Master in Science, Major in Anatomy, University of Michigan.

for any disease, sought to explain them as degenerating ganglion cells. Oppenheim, on the other hand, considered them as normal structures but gave no clear explanation of their significance. Staderini ('90) found the 'Herde' of Thomsen in the human oculomotor, trochlear, abducens, facial, and vagus nerves, and showed that these plaques were not to be considered as degenerating ganglion cells but as processes of neuroglia from the brain stem out into the nerve trunk. This he proved in serial cross-sections by tracing the continuity of the plaques with the central neuroglia. A. Hoche ('91) referring to the neuroglia, mentioned tooth-shaped processes extending from the surface of the spinal cord in company with the nerve fiber bundles and ending abruptly a little distance peripherally. Lavdowsky ('91) in his communication on the neuroglia of the spinal cord, referred to the same arrangement and pictured such a condition in figure 7 of plate 16 accompanying his article. E. Redlich ('92), in describing the lesions occurring in the spinal cord and posterior nerve roots in tabes dorsalis, said that the degeneration began in those fibers of the posterior root which were of the intramedullary type, thus intimating the presence of two essentially different types of nerve fibers, the intramedullary and the extramedullary. Both Kölliker ('93) and Edinger ('93) agreed with Lavdowsky in describing processes of neuroglia extending from the spinal cord out into the posterior roots of the spinal nerves. J. Schaffer (worked in '90, published in '94) found that the neuroglia in the nerve trunks ended in a pointed cone-shaped termination, convex peripheralward. Obersteiner and Redlich ('95), completing their work in '94, observed, during the course of their study of tabes dorsalis, a constriction and pial ring on the posterior nerve roots at their entrance into the spinal cord, and that a short distance peripherally the medullary sheaths lost their staining property over a small zone, resulting in a narrow clear space, a transverse 'Aufhellung,' which was bow-shaped with its convexity outwards. Obersteiner ('95) and E. Redlich ('97) defended and added details to their observations, urging especially the importance of the change from extramedullary to intramedullary

fibers in its relation to the primary lesions of tabes dorsalis in the spinal nerves. K. Schaffer ('01) added the observation that the myelin sheaths of the extramedullary part of the root stained darker but less sharply than those of the intramedullary portion, the two being separated by the convex, non-staining line which had already been described as the 'Aufhellung.' Obersteiner ('01) reviewed all the previous observations on the structure of the posterior roots of spinal nerves. E. Levi ('06) published the results of a comparative study of the sensory roots of all the spinal nerves, dealing especially with the transition from peripheral to central nerve fibers. E. Hülles ('06) extended the work of Levi to the human vagus, acoustic, and trigeminal nerves, finding there very much the same relations as in the posterior roots of the spinal nerves. Bikeles ('07) substantiated these histological findings from a physiological point of view by finding a difference between the reaction to secondary degeneration in the fibers peripheral to and central to the change. J. Bauer ('08) reported the results of a careful study of the posterior roots of spinal nerves in many animals; Primates, Ungulata, Carnivora, Insectivora, Rodentia, Edentata and Marsupalia. He found in all classes the same structures that had been described for the human spinal nerves.

MATERIAL AND METHODS

The brown rat (*Mus norvegicus*) was selected to furnish material because of the ease with which it could be handled and the readiness with which perfectly fresh nervous material could be removed. The trigeminal nerve root was selected primarily because of the fact that the feature under consideration is there particularly well shown; also because it is easily exposed and readily removed. Each root used was taken out in such a manner that a portion of the semilunar ganglion and a portion of the pons were included for landmarks and orientation. Similarly obtained nerves from the laboratory white rat, guinea-pig, rabbit, and dog furnished a series for a brief comparative study.

Standard laboratory methods were used in differentiating the histological elements studied. The general appearance was observed in formalin fixed sections stained in hematoxylin and one of the following counterstains—eosin, acid fuchsin, congo red, and Van Gieson's mixture (picro-fuchsin). The axones were studied in sections stained by Ranson's pyridine-silver method, and in a few Weigert myelin sheath preparations which showed a peculiar differential staining of the axis-cylinders.² The myelin sheaths were stained by Streeter's paraffin modification of the Weigert-Pal method, by osmium tetroxide, and by Haidenhain's iron-alum hematoxylin, following fixation in Bouin's and Yoshii's fluids. The neurolemma, pia mater, and connective tissue sheaths were studied in sections and teased preparations stained by Van Gieson's method and the common protoplasmic stains. Huber's modification of Benda's first method and Kingery's modification of the same were used to demonstrate the neuroglia.

The neuroglia sections were cut at a thickness of 4μ and 5μ . while all others were either 8μ or 10μ .

For the more intimate study of the myelin sheaths and neurolemma, nerve fibers which had been separated by teasing were studied. An attempt was always made to obtain both the peripheral and central types of fibers in the teased preparations, and they were examined in the fresh condition or following fixation and one of the stains enumerated above.

The embryology was studied from a set of serially-cut, sagittal sections of sixteen rat embryos, the use of which was granted through the courtesy of Professor G. Carl Huber.

PERSONAL OBSERVATIONS

Rat—Mus norvegicus

The sensory root of the trigeminal nerve averages about 4 mm. in length in fixed material. The motor root crosses the ventral surface of the sensory root obliquely from the median to the

² Smith and Mair state that diffuse staining of the myelin and deep staining of the axone in Weigert preparations is due to too long 'chromation.'

lateral side, the two being quite closely bound together. At a distance averaging from 1 mm. to 1.5 mm. from the brain stem the combined roots are apparently very slightly constricted, the diameter central to this zone being slightly less than the diameter peripheral to the constriction. In nerves which are brittle from fixation or dehydration there is a great tendency to fracture along the plane of this constriction, transverse to the long axis of the root.

In favorable longitudinal sections of the trigeminal nerve roots stained by a myelin method, there is, along a transverse line corresponding to the plane of the constriction, a distinct demarcation between a central lightly staining portion and a peripheral darkly staining portion. Between the two there is often a very narrow unstained zone extending transversely across the roots. This line of demarcation is usually somewhat saucer-shaped, appearing, in a longitudinal section of the root, as a curved line with the convexity peripheralward. The nerve fibers may be grouped in fairly distinct bundles which, in crossing this transition, project unequal distances beyond it, thus making of the change a serrate transverse line.

The root distal to this abrupt change shows the structure which by comparison is seen to be typical of peripheral nerve trunks, with the exception that the fibers are not found in definite funiculi each surrounded by perineurium. The component tissues of the trunk are definitely arranged, and in fixed and stained sections show good preservation of relations and structure.

The root proximal to this abrupt change is more characteristic of central nervous system tissue in that the myelin stains less intensely, the nerve fibers are not so firmly bound together, and in otherwise well preserved material often show distortion forms and are separated by spaces due to shrinkage.

Because of this abrupt change from the type of fiber found in the peripheral nerve trunk to the type found in the central nervous system, this region is particularly favorable for a detailed study of the comparative histology of central and peripheral medullated nerve fibers. Both types, which have been

subjected to identical fixation, sectioning, and staining, can be observed together in the same high power microscopic field.

It is generally difficult to trace in section the continuity of single nerve fibers across this transition line because of their tendency to suddenly change direction and thus disappear from the plane of section, and because of the fact that for a short distance the myelin sheaths often fail to stain, leaving a narrow clear zone between the central and peripheral areas. Our knowledge of the function of nerve fibers gives us the right to assume the continuity of these fibers, and actual proof may be obtained by teasing them through the line of transition.

The abrupt line of change in the motor root does not always correspond with that in the sensory root, and it may be either slightly central or slightly peripheral to the latter. The greater size of the sensory root as compared to the motor root so facilitates the sectioning of the desired region that most of the preparations were made from, and all the descriptions will be confined to, the sensory root of the trigeminal.

The supporting tissues bear a very important relation to the transition line. The pia mater forms a delicate fibrous sheath for the brain stem and extends outward along the nerve trunks for a short distance, becoming continuous with the epineurium which, farther peripherally, fuses with the denser dura mater. The junction between pia mater and epineurium is somewhat indefinite but may be arbitrarily placed at the constriction marking the line of change from peripheral to central nerve fibers. In the living condition the only constriction of which one can truly speak is a decrease in the diameter of the trunk central to the line of change as compared to the diameter peripheral to the transition. At the junction of the pia mater and epineurium there is often a ring of thickened connective tissue which shrinks during fixation and causes an annular constriction which is really an artifact. From this ring, fine trabeculae and bundles of white fibrous tissue pass through the nerve parallel to the line of transition, and together with the neuroglia form a very delicate frame-work for the support of the nerve fiber bundles. In the human these inward prolongations have

been described as forming a lamina cribrosa through which the nerve fiber bundles pass, but in the rat such a structure is not visible. Minute blood vessels often accompany these septae toward the interior of the nerve trunk.

The neuroglia can be traced from the brain stem out into the sensory root of the trigeminal as far as the transition line but never beyond. In the same manner that the neuroglia is more dense around the periphery of the brain stem just under the pia mater, so it forms a cortical or 'bark' layer around the trigeminal trunk. It is less extensively found in the center of the root. The general direction of the neuroglia fibers is at right angles to the nerve fibers, especially in the periphery of the trunk and in the lamina cribrosa region, but as observed in 4μ or 5μ sections the neuroglia tissue is not dense in any portion and takes less part in the formation of the supporting framework in the rat trigeminal than credited with in the human trigeminal. As previously indicated, the neuroglia and bundles of pia mater here and there extend distally from the transition line as pointed processes, and confer a distinctly serrated appearance upon this line. These prolongations rarely intermingle with the supporting tissue of the peripheral trunk, and processes of the latter extending centrally do not fuse with the pia mater and neuroglia. Upon this fact probably depends the tendency of the root to fracture along the line of change.

The supporting tissue of the peripheral nerve fibers consists of endoneurium; since there are no funiculi between the pons and semilunar ganglion in the trigeminal of the rat, there is no true perineurium. The neurolemma must be considered as a part of the framework and although it is an integral part of the peripheral nerve fibers it will be considered here. In sections it is usually difficult to differentiate between the endoneurium and neurolemma, and the most satisfactory method of studying them is in teased preparations. A variety of stains were applied to the teased nerve fibers, the most important being Weigert's myelin sheath stain, hematoxylin and Van Gieson's mixture, and osmium tetroxide. In teased specimens the endoneurium is seen to consist of delicate fibrils running close to and parallel

with the nerve fibers. White connective tissue fibrils are present to the exclusion of the yellow elastic. Even the white fibrils appear wavy after teasing operations in which they are stretched. The fibrils are accompanied by cells which are chiefly of the fixed or fibroblastic type. The protoplasm is rarely seen, and the nuclei vary in shape according to their position and the pressure of surrounding fibers. Their apparent shape varies with the angle at which they are viewed. In general they are oval or flattened, staining fairly intensively and possessing distinct chromatin granules.

The neurolemma forms a close investing sheath for the peripheral nerve fibers, and can be seen as a membrane only where the fiber is broken, or over a neurolemma nucleus, or sometimes at the nodes of Ranvier. The neurolemma nucleus is oval and has even larger chromatin granules than the nuclei of the endoneurium. It can be readily differentiated from the latter only when seen in profile, when it appears to lie on the side of the nerve fiber in an indentation in the myelin, between two nodes of Ranvier. The neurolemma is seen as a thin membrane covering it. In osmium tetroxide stains these nuclei are frequently surrounded by dark gray or black granules, called Elzholz granules.³ As mentioned before, the neurolemma and endoneurium stop abruptly at the transition line and do not intermingle with the pia mater and neuroglia.

It is interesting to compare the relative number of nuclei of all types found on the central and on the peripheral sides of the transition line. For this purpose 10μ sections stained in hematoxylin and eosin or acid fuchsin were used and the total number of nuclei in the same size microscopic fields each side of, and equally distant from, the transition line were counted by the aid of a ruled ocular. Using the number counted in a definite microscopic field central and adjacent to the transition line as unity, then the proportionate number in the same size field, adjacent to the transition peripherally, is expressed as a simple ratio. The table below, which gives the result of only four counts,

³ For a complete description of the cells found in peripheral nerve trunks see the article by Doinikow.

TABLE I

Showing the proportionate number of nuclei on the central and peripheral sides of the line of change in the sensory root of the trigeminal nerve of the rat

FIXATION	STAIN	THICKNESS	PROPORTION OF NUCLEI	
			Central	Peripheral
Formol.....	Hematoxylin and eosin	10	1	7.0
	Hematoxylin and eosin	10	1	8.3
Mueller.....	Hematoxylin acid fuchsin	10	1	6.2
	Hematoxylin and eosin	10	1	5.9

shows that the nuclei are more numerous on the peripheral side. The figures given are typically average.

The axones were first studied in differentially stained sections, but this was unsatisfactory because of the difficulty encountered in tracing them through the transition because of their abrupt change in course at that region. Their continuity can best be determined in fresh teased fibers or in teased material stained by osmium tetroxide. The axones pass through with no perceptible change in size and without exhibiting varicosities or constrictions. They show no characteristic difference in staining reaction on the two sides of the change.

The structure which presents the most interesting differences and variations in passing through the transition is the medullary sheath. Text-book descriptions give as the main morphological difference between peripheral and central nerve fibers, the absence of the neurolemma from the latter. It is true that this plays a rôle in their differentiation, but it is inconceivable that the presence or absence of neurolemma should determine all the differential features between central and peripheral fibers as observed in the rat trigeminal.

In the search for other morphological distinctions it is necessary to consider what is known as the 'neuro-keratin network.' This term has called forth much discussion. One group of writers maintains that the keratin-like network, insoluble in alcohol, which is seen in many Weigert myelin sheath preparations, is a preformed meshwork which serves as a support for the myelin during life. Another group contends that the network is purely an artifact, the result of the precipitation, from

colloidal suspension, of a certain chemical constituent which may be called neuro-keratin. A reasonable middle-ground, supported by the facts briefly mentioned below, is to assume the presence of a framework for the myelin and to consider the variations in size and arrangement of this framework to be artifacts dependent upon the methods of preparation. Although unable to substantiate any claim upon purely morphological studies, we must recognize that variations in the appearance of this framework in fixed nerve fibers may depend upon a varying chemical reaction, the result of differences in the fundamental arrangement of the substance in question, or the result of varying precipitation pictures due to the reaction of different reagents upon a uniform substance. In fixing trigeminal nerves previous to the application of Weigert's myelin sheath stain, it was found that the neurokeratin figure varied with the chemicals used or even with varying strengths of the same fixative. By rough handling or a long wait before fixation a very coarse network was secured, which in some cases presented the characteristic funnel-shaped bodies described by various authors. In the same way that Fischer ('99) worked out fixation pictures for many chemicals in their action upon protoplasm, definite pictures can be determined for the more characteristic fixatives in their action upon myelin. Conversely, the appearance of this network varies in fibers from the central and peripheral nervous systems when subjected to identical treatment. The best place to compare the two types of fibers is in a region showing an abrupt change from one to the other. In the sensory root of the trigeminal, where both the central and peripheral fibers have been handled identically in staining, the neuro-keratin network shows definite and rather uniform differences on the two sides of the transition. In the peripheral fibers there is usually a pronounced, regularly arranged, and fairly coarse meshed network. Because of this effective support the myelin sheath usually retains its tubular shape and is rather infrequently collapsed. The fibers therefore lie in quite close contact leaving few interstices in the peripheral root. On the other hand, the central fibers usually contain a loose, frail, irregularly

arranged meshwork of neurokeratin which does not prevent many of the fibers from collapsing. The resulting distorted fibers leave shrinkage spaces in the root central to the transition.

A slight difference in the diameter of the peripheral and the central fibers exists. This is emphasized beyond the normal proportion in Weigert myelin sheath stains, but is better represented in osmium tetroxide preparations in which the myelin is well preserved. In carefully teased specimens stained by the latter method, central and peripheral fibers from the same nerve were measured by means of camera lucida projection and a ratio determined between the measurements. From a series of such counts the average diameter of the central fibers in the nerves examined was found to be 8.2μ , with a range from 1.2μ to 12.5μ , while the average diameter of the peripheral fibers was 9.2μ , the range being from 1.2μ to 13μ . Taking the measurement of the central fibers as unity, the ratio of their diameter to that of the peripheral fibers is 1:1.12. This may be an exaggeration of their normal ratio during life, because we cannot state exactly the relative shrinkage effect of osmium tetroxide upon the two types. Further, these figures do not mean that there are no fibers smaller than 1.2μ , but rather that those were the smallest fibers which took the stain enough to be visible.

The relatively deeper staining of the peripheral myelin sheaths as compared with the central is well revealed in osmium tetroxide, Weigert myelin sheath, and Haidenhain's iron-alum hematoxylin preparations. This is the factor which really confers upon the sections the sharply defined line of change. A region such as we have under consideration is the most suitable place to demonstrate this difference because here it is possible to treat the two nerve fiber types by identical processes, thus ruling out the variations due to inevitable differences in method when treating two pieces of tissue separately. The difference in staining reaction in such sections is not one of quality so much as of degree or intensity. In osmium tetroxide both the central and peripheral myelin are stained brownish-black, but the peripheral is of an appreciably deeper shade. Of the possible explanations of this condition at least two natu-

rally suggest themselves. First, in mass staining the two different kinds of supporting tissue surrounding the fibers may so influence the penetration or bleaching of the stain as to bring about the result above noted. Second, the two shades may be the physical expression of actual chemical differences between central and peripheral myelin. When we remember that the reagent is identical, this explanation seems more possible. Moreover, in tissue which has been sectioned, the myelin is fully exposed to the action of the chemical, thus partially escaping the protective influence of the supporting tissues upon the reaction. The view that myelin in the central nervous system is deposited by a different agency than that in the peripheral system also lends support to the second explanation; but if myelin is everywhere deposited by the axones, it would be difficult to assign it a varying chemical constitution in different parts of the nervous system.

In many preparations there is a narrow clear space between the central and peripheral portions of the root, which is apparently due to an interruption of the myelin, the heavily staining peripheral sheath ending as a rounded cone through which the axone projects, passing through the narrow clear zone uncovered by myelin. In a few favorably cut fibers, myelin was seen to be reacquired on the central side at a distance of about 30μ from its interruption. A suggested explanation of this apparent lack of myelin in stained sections is that the supporting tissue of the lamina cribrosa region prevents the penetration of the stain to the myelin. This may be true in mass staining, such as with osmium tetroxide, but is less convincing when the same condition is found in preparations stained on the slide after sectioning. The view that myelin is deposited through the agency of different structures in the peripheral and central fibers and that there is a gap between these structures at the place under consideration might be advanced as an explanation of the phenomenon. If we accept the statement that all myelin is deposited through the agency of the axones, this explanation is less plausible. The fact that Bauer ('08) found this clear space to be inconstant in a large comparative series of the posterior roots of spinal nerves, makes its significance very obscure.

COMPARATIVE HISTOLOGY

The sensory roots of the trigeminal nerves of a short series of mammals were examined in order to gain an idea of the extent and character of this transition in the more common laboratory animals. The sections from the white rat (*Mus norvegicus albinus*) show exactly the same features as those from the brown rat described above, and outside the variations normally incident to a series of sections from one animal, there are no peculiarities to distinguish it from the wild variety. In the guinea-pig preparations the only constant difference noticeable is the slightly greater curve of the transition line, which forms a peripherally directed cone with rounded apex. This animal furnishes good nerve material for the application of the neuroglia staining technique as modified by Huber for use with mammals other than human. In the rabbit trigeminal the connective tissue lamina cribrosa is more pronounced and bundles of fibrous tissue can often be seen running at right angles to the nerve fibers. The transition forms more nearly a straight line. The nerve fibers are grouped into bundles which are more definite than those of the rat. The line of change is relatively the same distance from the brain stem as in the wild rat. The dog shows a very distinct and abrupt change from peripheral to central type of fibers. The transition line is relatively near the brain when its position is compared with the diameter of the trunk. Instead of always showing a simple outwardly convex line, the curve is often doubly convex or bow-shaped with both convexities directed peripherally. The contrast in staining on the two sides is very pronounced.

EMBRYOLOGY

The work of Harrison and others has taught us that the nerve fibers grow out from their neuroblast cell bodies by direct extension, and become anchored in their permanent position at an early stage of development. The sensory roots of all nerves develop from the neural crest, the neuroblasts in the latter sending processes centrally to the spinal cord and peripherally to the region of the future sensory ending. Harrison ('04) has

showed us that the extension of these processes is accompanied by the migration of certain cells from the crest which give rise to the neurolemma sheath cells or Schwann cells.

In sections of the neural tube and semilunar ganglion anlage in a rat embryo of 6 mm. length (crown-breech) the centrally directed processes of the neural crest cells can be traced into the marginal layer of the neural tube, passing through the external limiting membrane. Accompanying this definite embryonic nerve trunk are numerous cells with small, oval, lightly staining nuclei interspersed between the fibers. These extend only as far as the anlage of the pia mater and to the external limiting membrane which lies closely adherent to the marginal layer and is formed by the interweaving of the peripheral process of the spongioblasts. Along this line these cells cease abruptly in a curve corresponding to the normal surface curve of the brain stem. These nuclei belong chiefly to the developing sheath cells which apply themselves to the sides of the growing axones. In a 6 mm. rat embryo they are fairly evenly distributed in the trunk and in a 10 mm. embryo they have surrounded all the fibers, but together with the ingrowing mesodermal cells have also gathered into rows in many parts of the trunk, marking the development of fiber bundles.

In distinction to the peripheral trunk, the marginal layer of the neural tube shows a less intense staining reaction. This is primarily due to the almost complete absence of nuclei and cannot be assigned at this time to different types of myelin, because such a chemical substance is not present. Its acquisition at a later stage accentuates the differential staining. This early line of change from peripheral to central fibers corresponds to the pia mater anlage and external limiting membrane, both of which must be pierced by the developing axones in their exit or entrance, and which act as a barrier to the ingress of the sheath cells.

These relations persist and may be demonstrated in sections of increasingly older embryos. During the further development, the nerve trunk becomes better differentiated from the surrounding mesenchyme, the sensory root is relatively longer

compared with its diameter, and the nerve fibers become more definitely grouped in bundles as the supporting tissue assumes definite arrangement. In an 18 mm. rat embryo the pia mater is a definite membrane and is separated from the denser anlage of the dura mater by a slight amount of loose-meshed tissue, the arachnoid anlage. At this stage the semilunar ganglion lies close to the pons on the one side and to the bony foramina for its divisions on the other so the whole trunk is relatively short. During the development of the skull, when the distance from the foramina for the trigeminal divisions to the attachment of the sensory root on the pons is gradually increasing, it is conceivable that enough tension is put upon the roots to cause the line of change, representing the original line of pia mater and external limiting membrane, to be drawn slightly away from the surface of the brain in an outwardly convex bow. This view is substantiated when we examine sections of a 23 mm. rat embryo in which the arachnoid tissue surrounding the trigeminal root is relatively much increased because of the greater distance between the pia mater and dura mater along the course of the nerve. The effect is seen in a section of a 30 mm. rat embryo where the transition line, even before birth, is slightly external to the brain surface. The migration of this line, due to inequality between growth in the nerve roots and in the skull, takes place chiefly in the early post-natal period, because it is slightly established in a 30 mm. embryo and shows well in a young rat about four weeks after birth. The position of this line of change may be regarded as the result of varying degrees of, or the lack of, traction upon the trunks during the rapid development of the body which causes separation of the attached ends of the nerve at a slightly greater rate than compensated by the growth of the fibers themselves.

For the practical importance attached to this transition line in its relation to the etiology of *tabes dorsalis*, the reader is referred to the articles by Nageotte, Obersteiner and Redlich, Levi, and the authors cited by them.

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CONCLUSIONS

1. In the sensory root of the trigeminal nerve of the rat (*Mus norvegicus*), about 1 mm. from the pons, is an outwardly convex line which marks an abrupt change from the peripheral to the central type of nerve fibers.

2. The peripheral supporting tissues, endoneurium and epineurium, together with the neurolemma, meet, without intermingling, the central supporting tissues, neuroglia and pia mater, to form an indefinite lamina cribrosa through which the bundles of nerve fibers pass.

3. The axones extend through this change uninterruptedly and unaffected morphologically.

4. The peripheral myelin shows—

a. A deeper coloration than the central when both are identically treated with myelin stains.

b. A 'neuro-keratin network' which is more prominent and more regular than that in the central fibers when both are identically treated.

These facts may be interpreted as showing distinct chemical and physical differences between the central and peripheral myelin.

5. A number of other mammals show a similar or identical picture in the sensory roots of their trigeminal nerves.

6. This change may be considered as occurring at the line where the pia mater and external limiting membrane surrounding the embryonic nervous tube were pierced by the growing processes of neuroblasts, these membranes acting as barriers against the entrance of sheath cells into the neural tube. The position of this line depends upon the amount of tension to which the root is subjected during development.

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ADVANTAGES OF SAGITTAL SECTIONS OF PIG EMBRYOS FOR A MEDICAL EMBRYOLOGY COURSE¹

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EIGHT FIGURES

The writer has recently been impressed with the superiority of sagittal sections over transverse sections for most of the laboratory work of medical students in embryology. By the time the ordinary student has familiarized himself with the various turns found in a transverse series and has determined the direction required to follow forward or backward one of the three or four sections of the same organ found in a single transverse section, a considerable portion of the short time allotted for this course has elapsed. Since the time is insufficient for the student making graphic or wax reconstructions of the various systems, the little knowledge obtained by student, when only transverse sections are supplied, is usually acquired from a study

¹ It is assumed in most medical embryological laboratories that pre-medical students have had work in maturation, fertilization, segmentation and the early development of the main systems in some vertebrate. The aim of a medical course then is to obtain in as short time as possible a fairly comprehensive understanding of the formation of the various structures and organs of the body. To accomplish this the student should have access to a number of different stages of human embryos and their placenta, and to a collection of cleared embryos that will show the formation of the skeleton. In our laboratory every two students are supplied with a slide box containing a longitudinal and a transverse series of a 6 mm. pig embryo, a transverse section of a 12 mm. pig, twelve specially selected transverse sections of a 25 mm. pig and two 15 mm. pigs for dissection of the viscera, central nervous system and the cranial nerves. The writer is an advocate of the method of taking up the laboratory work from the standpoint of one system at a time, rather than attempting the study of all systems simultaneously.

of the laboratory models or from his general didactic instruction rather than from a study of his transverse sections.

It must be admitted, however, that for certain special studies, as for example, the origin and distribution of the cranial and spinal nerves, the organs arising from the branchial arches, certain relationships of the heart chambers and the formation of the vertebrae, transverse sections should be consulted. To amplify further, a transverse section through the otocyst of a 6 or 12 mm. pig embryo, which is a more or less frontal section through the rhombencephalon, affords an excellent view of the cranial nerves and their ganglia. Likewise certain transverse sections in the trunk region, especially of 20 and 25 mm. embryos, will give excellent pictures of the spinal nerve components and the various elements that go to make up a vertebra.

All of the illustrations for this paper were taken from a single sagittal series of a 6 mm. pig embryo, belonging to a student's loan set.

ALIMENTARY CANAL

A study of the development of the alimentary canal and the formation of its appendages is one of the first studies that can be made satisfactorily from an examination of a sagittal series of a 6 mm. pig. If the student will examine a median sagittal section through the pharynx region he will be able to follow the course of the digestive tract from the oral cavity to the branching off of the lung bud, and from especially favorable sections (fig. 1) this tube can be seen in section from the oral cavity to the outbudding of the dorsal pancreas. From its dorsal wall the following protuberances have appeared, enumerated from before backward: Rathke's pocket (*R.P.*) and its relationship to the infundibulum, Sessel's pocket (*S.P.*) and the dorsal pancreas (*D.Pan.*) The following ventral evaginations are shown: Thyroid gland (*Thyr.*) situated near the external carotid artery, the trachea bud (*Tr.*) from its origin to its separation into the two bronchi, the gall bladder (*G.Bl.*) and the hepatic portion of the liver (*Liv.*). The student should make an outline sketch of this section, incorporating in it the above mentioned portions of the alimentary canal. An examination of a few following sec-

tions brings us to the section from which figure 2 was drawn. From such a section the student can supply the cephalic arm of the intestinal loop (*Int.*) to his drawing of the digestive tract, and a few sections more (fig. 3) will supply a large portion of the caudal arm of the intestinal loop and the caudal end of the intestine (*Int.*) nearly to the cloaca. This section (fig. 3) also shows the position of the distal end of the ventral pancreas (*V.Pan.*), which can be readily followed from adjacent sections to its origin from the intestine at the point of the budding off of the gall bladder. When the caudal portion of the intestine has been added to the drawing of the digestive tract, the student has obtained a very satisfactory picture of the embryonic digestive tube and a number of its appendages from a study of three sagittal sections of a 6 mm. pig embryo. The cloaca end of the alimentary canal can also be studied from this series but will be taken up under the next subdivision.

URINARY SYSTEM

Any of the lateral sections of this 6 mm. sagittal pig series will show the extent and structure of the mesonephros. From figure 4, which is a sagittal section through the cephalic end of the mesonephros, it is clear that the mesonephros (*Meson.*) is composed of collecting tubules, glomeruli and a mass of undifferentiated mesenchyme.

In most sagittal series of pig embryos the extreme lateral sections are almost as perfect transverse sections through the tail or cloaca region as those from a frontal series and are far superior to corresponding sections from a transverse series. It is apparent that a few perfectly true transverse sections through the cloaca region will give the student a very clear conception of the relationship of the various ducts of the embryonic kidney; while it is equally true that nothing can be more confusing than an equal number of oblique transverse sections through this region. In figure 5, which is a more lateral section of the same sagittal series as figures 1 to 4 we have a nearly transverse section through the cephalic end of the cloacal (*Cl.*) expansion of the intestine. In this section both of the mesonephric or

Wolffian ducts are cut transversely and the left one (*L.W.D.*) is about to empty into the cloaca. It is from this region in a 7 mm. pig that the metanephric ducts or ureters bud off from the mesonephric or Wolffian ducts. Ventrally the allantois (*Al.*) is leaving the cloaca to enter the umbilicus. A more lateral section (fig. 6), which is through a more caudal region of the cloaca than figure 5, shows the left mesonephric or Wolffian duct *L.W.D.* emptying into the cloaca. In a still more lateral section (fig. 7) the right mesonephric or Wolffian duct (*R.W.D.*) will be seen terminating in the cloaca, which is rapidly diminishing in size to become the postgut in figure 8 (*P.G.*). In figures 6 to 8 the allantois (*Al.*) has entered the umbilicus with the umbilical blood vessels and is situated midway between the two umbilical arteries.

BLOOD VESSELS

Sagittal sections are especially useful for a study of the general arrangement of the principal blood vessels, which in general run for long distances in a longitudinal direction.

Veins

A slightly lateral sagittal section (fig. 4) furnishes an excellent view of the main venous trunks of a 6 mm. pig. The right atrium (*R.At.*), ventricle (*R.Ven.*) and the conus or bulbus arteriosus are seen in their correct position. This section is a little to the right of the atrio-ventricular opening. The sinus venosus (*S.V.*) will be seen opening into the right atrium, its orifice being partly guarded by the sinu-atrial valves (*S.A.V.*) The endothelial lining of the heart chambers is clearly shown and the cardiac muscle is in an early stage of its histogenesis.

From figure 4 it is clear that the sinus venosus receives the entire venous blood from the embryo and the entire arterial supply from the fetal placenta. Entering the sinus venosus from above, the short right ductus Cuvieri or common cardinal vein (*R.D.C.*) is formed from the union of the right anterior cardinal vein (*R.A.C.V.*), with the right posterior cardinal vein (*R.P.C.V.*). The former comes from the head and neck and the

latter collects the intersegmental veins (*Ints. V.*) from the body walls, the mesonephric veins from the mesonephros and a sub-cardinal vein (*Sub. C. V.*) traversing the ventral surface of the mesonephros. From below the left ductus Cuvieri or common cardinal vein (*L. D. C.*) joins the sinus venosus, and after curving around the lower and left side of the pharynx it takes origin from the union of anterior and posterior cardinal veins from the left side of the body. Not far from its termination in the sinus venosus the left ductus Cuvieri receives the left umbilical vein (fig. 1, *L. Umb. V.*). The terminal portion of this vein probably represents the terminal portion of the original omphalo-mesenteric vein. From the rear the sinus venosus is continuous with a large sinusoid (*S*), which might be designated as a part of the ductus venosus, but which probably represents an enlargement of the original proximal or terminal portion of the right omphalo-mesenteric vein. Sinusoid (*S*) collects the portal or common omphalo-mesenteric vein (*P. V.*) and the right umbilical vein (*R. Umb. V.*) from the rear, the former being somewhat more dorsal in position. Toward the median line sinusoid (*S*) is continuous with a large transverse sinusoid, the ductus venosus, which extends transversely through the cephalic end of the liver to communicate with the left umbilical vein. The position of the ductus venosus is shown in figures 2 and 3 (*D. V.*) to be more dorsal on the right side than on the left, which has doubtless been brought about by the difference in level of its two terminal connections, sinusoid (*S*) and the sinus venosus on the right side and the left umbilical vein and left ductus Cuvieri on the left side.

A comparison of the two umbilical veins reveals the left one to be slightly the larger. After entering the lower left corner of the liver the left umbilical, pursues a fairly straight course through the first half of the liver, to finally bend dorsad and cephalad to terminate in the left ductus Cuvieri (fig. 1, *L. D. C.*). As previously stated the left umbilical vein is also in direct communication with the sinus venosus through the ductus venosus. The opening of the left umbilical vein into the left ductus Cuvieri is fully as large as its communication with the ductus venosus, so that the blood in the left umbilical vein would have an option

of two ways of reaching the sinus venosus and the heart. Also the blood in the right side of the liver, collected in sinusoid (*S*) could easily find its way into the sinus venosus by way of the ductus venosus and the left ductus Cuvieri. The right umbilical vein will be seen in the lateral sagittal sections 5 and 6 (*R. Umb.V.*) to traverse the lateral wall of the abdomen a little below the level of the mesonephros and to enter the umbilicus in the region of the cloaca. Likewise corresponding sections on the left side of this embryo would show a similar distribution of the left umbilical vein. Upon entering the umbilicus the umbilical veins are situated laterally to their corresponding arteries (figs. 5 and 6), but soon assume a caudal position (fig. 7, *R. Umb.V.* and *R. Umb.A.*). A still more lateral section (fig. 8 shows the umbilical veins have united more distally in the umbilicus to form a common umbilical vein (*Umb.V.*).

In addition to the connection between the two umbilical veins through the liver, the ductus venosus, there is a smaller anastomosing vein between the two umbilicals behind the liver. It appears (figs. 2 and 3, *A.V.*) in the mesenchyme directly below the pancreas, midway between the liver and the cephalic arm of the intestinal loop.

The portal vein (fig. 3, *P.V.*), representing in part the combined omphalo-mesenteric veins, occupies a general median position a little to the right of the digestive tract. In figure 3 it will be seen passing between the dorsal and the ventral pancreas to enter the caudal surface of the liver slightly median and dorsal to the right umbilical vein. These two veins are portrayed in figure 4 as anastomosing inside the liver, the common trunk after expanding into sinusoid (*S*) enters the sinus venosus from the rear. A short distance behind the dorsal pancreas (fig. 1) the portal vein takes origin from the union of the superior mesenteric vein with the omphalo-mesenteric vein. The former (*Mes.V.*) comes from the caudal region and the latter (fig. 2, *O.M.V.*) passes dorsad in front of the cephalic arm of the intestinal loop and represents the original right omphalo-mesenteric vein. At the junction of the omphalo-mesenteric vein with the superior mesenteric vein to form the portal vein,

a small branch is received from the region of the pancreas. It likely represents a persisting portion of the original left omphalo-mesenteric vein. There is a communicating vein between the portal and subcardinal veins.

Arteries

Excepting in the extreme cephalic and caudal extremities of a 6 mm. pig embryo the originally paired dorsal aortae have fused and formed a median longitudinal trunk of considerable size, the aorta. Most any median sagittal section of this series (fig. 3) will show long stretches of the aorta (*Ao.*) situated below the notochord and extending out laterally beyond the limits of the spinal cord. In figure 4 a portion of the original right dorsal aorta, now the right internal carotid artery (*Ao.*), is present in connection with the third branchial artery. Figures 1 and 2 show the intersegmental arteries (*Ints.A.*) to be well-advanced. It will be seen from figures 2 and 3 that the omphalo-mesenteric artery (*O.M.A.*) takes origin from the aorta from three stems, which soon unite in a single trunk that passes ventrally between the two arms of the intestinal loop. The bulbus or conus arteriosus (*C.A.*) and the ventral aorta (*V.Ao.*) are cut more or less longitudinally in figures 1, 2 and 3. In figure 2 the basal portion of the third, fourth and the sixth or fifth right branchial arteries are present in connection with the ventral aorta, and nearly the entire course of the right sixth or fifth branchial artery (*Br.A. 5*) can be followed from the ventral aorta to the right dorsal aorta. In figure 3 a considerable of the right fourth branchial artery (*Br.A. 4*), especially the distal portion terminating in the right dorsal aorta, is seen between the third and fourth branchial clefts. A similar portion of the right third branchial artery (*Br.A. 3*) empties into the right dorsal aorta or external carotid artery (*Ao.*) in figure 4. In figure 1 a small portion of the right external carotid artery (*E.Car.A.*) appears in the region of the thyroid gland. The pulmonary and subclavian arteries are not shown in any of the sections figured. They are best followed in transverse sections.

CENTRAL NERVOUS SYSTEM

In most any median sagittal section of a 6 mm. pig embryo, as figure 1, the primary, secondary and tertiary segmentation of the neural tube can be readily distinguished. The neuromeres (*Neuro.*) or primary segments are clearly defined in the medulla region. Concerning the secondary segments of the brain region, the forebrain occupies all the space in front of the dotted line between the cavities (*Dien.*) and (*Mes.*), the midbrain corresponds to the division (*Mes.*) and the remaining portion of the brain behind the mesencephalon (*Met.* and *My.*) represents the hindbrain. The tertiary segments- telencephalon (*Tel.*), diencephalon (*Dien.*), mesencephalon (*Mes.*), metencephalon (*Met.*) and myelencephalon (*My*) are well-differentiated in this section. The boundry line between the diencephalic and telencephalic segments, as determined by Johnston for early embryos, is a line between the velum transversum (*V.T.*) and the postoptic recess (*P.O.R.*) or between the caudal borders of the interventricular foramen and the optic chiasma for later stages. The following diverticula appear in the basal plate of the diencephalon- mamillary recess (*M.R.*), infundibular recess (*I.R.*), post-optic recess (*P.O.R.*) and the preoptic recess (shown in front of the postoptic recess and the optic chiasma thickening). In the telencephalon the expansion of the hemispheres (*C.H.*) is apparent, but is more conspicuous in more lateral sections (fig. 3). The roof plate of the rhombencephalon (metencephalon and myelencephalon) is for the most part reduced to one layer of flattened cells, the mesoderm outside is vascular and there is considerable stained coagulum within the fourth ventricle, giving every indication that the roof plate (tela chorioidea) has attained the function of producing cerebro-spinal fluid. The cervical (*Cer.F.*) and cephalic (*Ceph.F.*) flexures are prominent in this section, but the pontine flexure (*Pon.F.*) is barely visible. Concerning the histogenesis of the central nervous system (figs. 1 to 4) show an early differentiation of the neural tube into ependymal, mantle and marginal layers, and the germinal cells are proliferating rapidly about the ventricles and the central canal.

SOMITES

To illustrate the early differentiation of the somites into myotome and sclerotome, the extreme lateral sections of this series, which are nearly transverse sections through the tail, are especially valuable, for the reason that the caudal somites are in a much more elementary state than the cephalic somites. In such a section (fig. 8) the central cavity of the right somite is filled with spindle-shaped cells that migrated from the walls of the somite. From the somite on the opposite or left side of this section it will be seen that this migration took place mainly from the median and ventral walls of the somite. These diffuse spindle-shaped cells, the future sclerotome (*Scl.*), are about to migrate medially to envelop the notochord and the spinal cord to form the skeletal axis. The outer or more dense portion, the myotome (*Myo.*) has differentiated into myoblasts and muscle fibrils in a more cephalic region (fig. 3, *Myo.*). Also the neighboring sclerotomes (*Scl.*) have differentiated into dense and diffuse portions, preparatory to the formation of the membranous vertebrae. It is obvious that later stages are necessary for the further study of the development of the vertebrae and trunk muscles.

PLATE 1

EXPLANATION OF THE FIGURE

1 Median sagittal section of a 6 mm. pig embryo (Class series No. 4, U. O. M.S.). This section shows the cephalic end of the digestive tract and diverticula from the oral cavity to the dorsal pancreas, and is a median sagittal section through the brain. It passes through the left side of the heart, displays the left umbilical vein terminating in the left ductus Cuvieri and shows the origin of the portal vein from the superior mesenteric and omphalo-mesenteric veins.
 X 26

ABBREVIATIONS

<i>Ao.</i> , aorta	<i>My.</i> , myelencephalon
<i>Ceph.F.</i> , cephalic flexure	<i>Neuro.</i> , neuromeres
<i>Cer.F.</i> , cervical flexure	<i>Oes.</i> , oesophagus
<i>C.H.</i> , cerebral hemispheres or pallium	<i>O.M.V.</i> , omphalo-mesenteric vein
<i>Coe.</i> , coelom	<i>P.C.</i> , posterior commissure
<i>C.Q.</i> , corpora quadrigemina	<i>Per.C.</i> , pericardial cavity
<i>Crb.</i> , cerebellum	<i>Phar.</i> , pharynx
<i>Dien.</i> , diencephalon	<i>Pon.F.</i> , pontine flexure
<i>D.Pan.</i> , dorsal pancreas	<i>P.O.R.</i> , postoptic recess
<i>E.Car.A.</i> , external carotid artery	<i>P.V.</i> , portal vein
<i>End.C.</i> , endocardial cushion	<i>R.P.</i> , Rathke's pocket
<i>G.Bl.</i> , gall bladder	<i>Som.</i> , somatopleure
<i>Int.</i> , intestine	<i>S.P.</i> , Sessel's pocket
<i>I.R.</i> , infundibular recess	<i>Sp.Cd.</i> , spinal cord
<i>Isth.</i> , isthmus	<i>Spl.</i> , splachnopleure
<i>L.At.</i> , left atrium	<i>S.Tr.</i> , septum transversum
<i>L.D.C.</i> , left ductus Cuvieri	<i>Tel.</i> , telencephalon
<i>Liv.</i> , liver	<i>Tela.</i> , tela chorioidea
<i>L.Umb.V.</i> , left umbilical vein	<i>Thyr.</i> , thyroid
<i>L.Ven.</i> , left ventricle	<i>T.P.</i> , tuberculum posterius
<i>Mes.</i> , mesencephalon	<i>Tr.</i> , trachea bud
<i>Mes.V.</i> , superior mesenteric vein	<i>Umb.</i> , umbilicus
<i>Met.</i> , metencephalon	<i>V.Ao.</i> , ventral aorta
<i>M.R.</i> , mamillary recess	<i>V.T.</i> , velum transversum

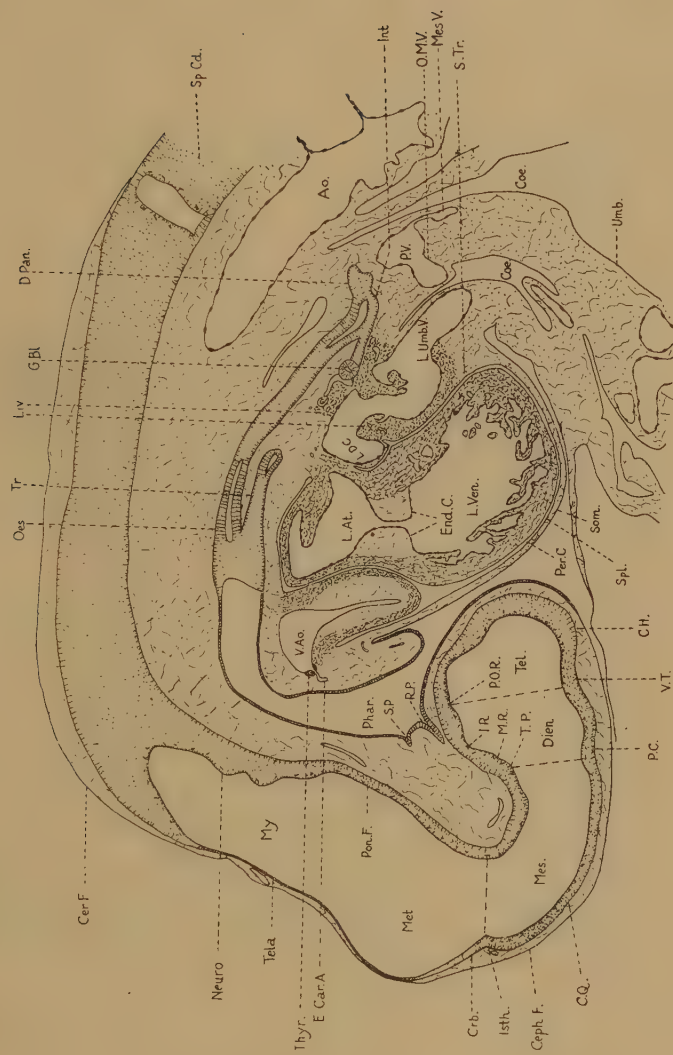


PLATE 2

EXPLANATION OF THE FIGURE

2 Sagittal section 111 microns to the right of figure 1, introduced to show: the cephalic arm of the intestinal loop, the ductus venosus, the anastomosing vein between the umbilical veins behind the liver, position of the omphalo-mesenteric vein and the aorta, source of the omphalo-mesenteric artery, and course of the sixth or fifth branchial artery. $\times 26$

ABBREVIATIONS

<i>Ao.</i> , aorta	<i>Liv.</i> , liver
<i>A.V.</i> , anastomosing v. between umb.	<i>L.Ven.</i> , left ventricle
<i>v-s</i>	<i>Mes.</i> , mesencephalon
<i>Br.</i> , bronchus bud	<i>Met.</i> , metencephalon
<i>Br.A.3.</i> , third branchial artery	<i>Neuro.</i> , neuromeres
<i>Br.A.4.</i> , fourth branchial artery	<i>O.M.A.</i> , omphalo-mesenteric artery
<i>Br.A.5.</i> , sixth or fifth branchial a.	<i>O.M.V.</i> , omphalo-mesenteric vein
<i>Coe.</i> , coelom	<i>Per.C.</i> , pericardial cavity
<i>Crb.</i> , cerebellum	<i>Phar.</i> , pharynx
<i>Dien.</i> , diencephalon	<i>P.V.</i> , portal vein
<i>D.Pan.</i> , dorsal pancreas	<i>R.P.</i> , Rathke's pocket
<i>D.V.</i> , ductus venosus	<i>S.P.</i> , Sessel's pocket
<i>G.Bl.</i> , gall bladder	<i>Sp.Cd.</i> , spinal cord
<i>Int.</i> , intestine	<i>Sp.G.</i> , Spinal ganglion
<i>Ints.A.</i> , intersegmental artery	<i>Tel.</i> , telencephalon
<i>L.At.</i> , left atrium	<i>Umb.</i> , umbilicus
<i>L.D.C.</i> , left ductus Cuvieri	<i>V.Ao.</i> , ventral aorta

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PLATE 3

EXPLANATION OF THE FIGURE

3 Sagittal section 113 microns to the right of figure 2. It shows part of the caudal arm of the intestinal loop and the caudal end of the intestine to the cloaca, the relation of the dorsal pancreas to the ventral pancreas, entire length of the portal vein from its source to its termination in sinus (*S*) within the liver, the ductus venosus and the anastomosing vein between the two umbilical veins behind the liver, nearly all of the aorta, parts of the third, fourth and sixth or fifth branchial arteries, and several of the cephalic myotomes and sclerotomes.

× 26

ABBREVIATIONS

<i> Ao.</i> , aorta	<i> Liv.</i> , liver
<i> A.V.</i> , anastomosing v. between umb.	<i> Mes.</i> , mesencephalon
<i> V-S</i>	<i> Myo.</i> , myotome
<i> Br.</i> , bronchus bud	<i> Neuro.</i> , neuromeres
<i> Br.A.3</i> , third branchial artery	<i> O.M.A.</i> , omphalo-mesenteric artery
<i> Br.A.4.</i> , fourth branchial artery	<i> Per.C.</i> , pericardial cavity
<i> Br.A.5</i> , sixth or fifth branchial a.	<i> Phar.</i> , pharynx
<i> Br.C.2</i> , second branchial cleft	<i> P.V.</i> , portal vein
<i> Br.C.3</i> , third branchial cleft	<i> R.At.</i> , right atrium
<i> C.A.</i> , conus or bulbus arteriosus	<i> R.Ven.</i> , right ventricle
<i> Coe.</i> , coelum	<i> Scl.</i> , sclerotome
<i> Dien.</i> , diencephalon	<i> Sp.Cd.</i> , spinal cord
<i> D.Pan.</i> , dorsal pancreas	<i> Sp.G.</i> , spinal ganglion
<i> D.V.</i> , ductus venosus	<i> S.Tr.</i> , septum transversum
<i> G.Bl.</i> , gall bladder	<i> Tel.</i> , telencephalon
<i> Int.</i> , intestine	<i> Tela.</i> , tela chorioidea
<i> L.D.C.</i> , left ductus Cuvieri	<i> V.Pan.</i> , ventral pancreas

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PLATE 4

EXPLANATION OF THE FIGURE

4 Sagittal section 180 microns to the right of figure 3, which is considerably to the right of the median line, passing through the entrance of the sinus venosus into the right atrium. It shows nearly all of the principal veins of the right side, the portal vein and the left ductus Cuvieri emptying into the sinus venosus; also a portion of the original right dorsal aorta, now the right internal carotid artery, is present in connection with the third branchial artery. X 26

ABBREVIATIONS

<i>Am.</i> , amnion	<i>Phar.</i> , pharynx
<i>Ao.</i> , aorta	<i>P.V.</i> , portal vein
<i>Br.A.3</i> , third branchial artery	<i>R.A.C.V.</i> , right anterior cardinal vein
<i>Br.C.1</i> , first branchial cleft	<i>R.At.</i> , right atrium
<i>Br.C.2</i> , second branchial cleft	<i>R.D.C.</i> , right ductus Cuvieri
<i>Br.C.3</i> , third branchial cleft	<i>R.P.C.V.</i> , right posterior cardinal vein
<i>C.A.</i> , conus or bulbus arteriosus	<i>R.Umb.V.</i> , right umbilical vein
<i>C.H.</i> , cerebral hemisphere or pallium	<i>R.Ven.</i> , right ventricle
<i>Coe.</i> , coelom	<i>S.</i> , large sinusoid emptying into the sinus venosus
<i>Gl.</i> , glomerulus	<i>S.A.V.</i> , sinu-atrial valves
<i>Ints.V.</i> , intersegmental vein	<i>Som.</i> , somatopleure
<i>L.D.C.</i> , left ductus Cuvieri	<i>Spl.</i> , splanchnopleure
<i>Liv.</i> , liver	<i>Sub.C.V.</i> , subcardinal vein
<i>Meson.</i> , mesonephros	<i>S.V.</i> , sinus venosus
<i>Myo.</i> , myotome	<i>Umb.</i> , umbilicus
<i>Ot.</i> , otocyst	
<i>Per.C.</i> , pericardial cavity	



PLATE 5

EXPLANATION OF THE FIGURE

5 Sagittal section considerably lateral to those from which figures 1 to 4 were drawn. This section is a sagittal section through the right mesonephros and the right umbilical vein, but a nearly transverse section through the tail region at the level of the beginning of the umbilicus and cloaca. Note that the left umbilical artery and vein have entered the umbilicus and the right artery and vein are entering it. Observe that the cloaca, mesonephric or Wolffian ducts are cut in transverse section and the allantois is in connection with the cloaca. $\times 26$

6 Sagittal section but 50 microns to the right of figure 5. Observe that the allantois has lost its connection with the cloaca and is situated midway between the umbilical arteries in the umbilicus; also that the left mesonephric or Wolffian duct has joined the cloaca. $\times 26$

ABBREVIATIONS

<i>Al.</i> , allantois	<i>Nc.</i> , notochord
<i>Cl.</i> , cloaca	<i>R.Umb.A.</i> , right umbilical artery
<i>L.Umb.A.</i> , left umbilical artery	<i>R.Umb.V.</i> , right umbilical vein
<i>L.Umb.V.</i> , left umbilical vein	<i>R.W.D.</i> , right Wolffian or mesonephric duct
<i>L.W.D.</i> , left Wolffian or mesonephric duct	<i>Sp.Cd.</i> , spinal cord
<i>Meson.</i> , mesonephros	<i>Umb.</i> , umbilicus
<i>Myo.</i> , myotomes	

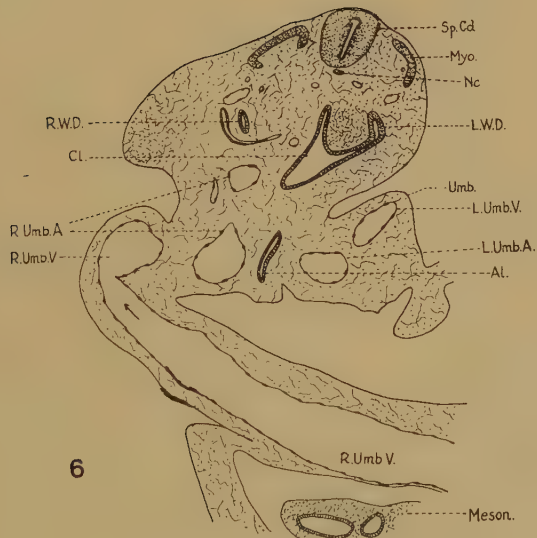
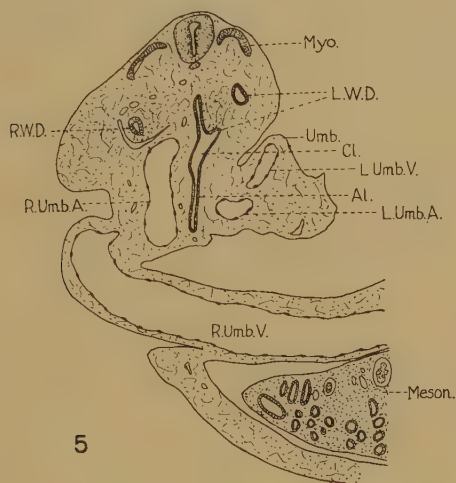


PLATE 6

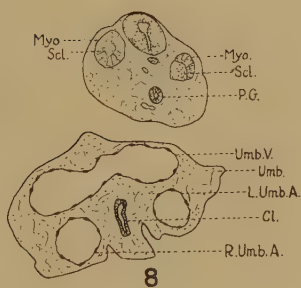
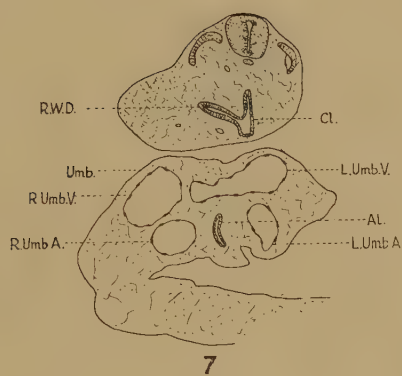
EXPLANATION OF THE FIGURES

7 Sagittal section 200 microns to the right of figure 6, a more caudal section through the embryo and a more ventral or distal section through the umbilicus. Observe that the umbilicus has nearly lost connection with the embryo, that the umbilical veins are situated behind their corresponding arteries and are about to anastomose. The right mesonephric or Wolffian duct will be seen terminating in the cloaca, which has become much reduced in caliber. $\times 26$.

8 Sagittal section 220 microns lateral to figure 7, a more caudal transverse section of the embryo and a more distal transverse section of the umbilicus. Note that the umbilical veins have united in a common vein and the reduction in size of the digestive tract from the cloaca to a small postgut. $\times 26$

ABBREVIATIONS

<i>Al.</i> , allantois	<i>R.Umb.V.</i> , right umbilical vein
<i>Cl.</i> , cloaca	<i>R.W.D.</i> , right mesonephric or Wolffian duct
<i>L.Umb.A.</i> , left umbilical artery	<i>Scl.</i> , sclerotome
<i>L.Umb.V.</i> , left umbilical vein	<i>Umb.</i> , umbilicus
<i>Myo.</i> , myotome	<i>Umb.V.</i> , umbilical vein (in umbilicus)
<i>P.G.</i> , postgut	
<i>R.Umb.A.</i> , right umbilical artery	



ON THE BRANCHIAL EPITHELIUM OF AMMOCOETES¹

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EIGHT FIGURES (TWO PLATES)

In a recent investigation of the thymus in *Ammocoetes* ('17) it occurred to the author that the branchial epithelium of the advanced larva does not represent a pure endodermal epithelium. The characters that suggested this hypothesis may be enumerated as follows: The epithelium in the young larva (5 mm.) is represented by a distinct single layer of cells which is sharply marked off from the underlying mesenchyma (fig. 1). In slightly older larvae the epithelium of the gill arches has acquired a somewhat stratified character resembling transitional epithelium as found in the bladder of mammals (fig. 8). In still later stages the epithelium of the gill lamellae is composed of a mass of cells which are not arranged in stratified layers (figs. 6 and 7). Mesenchyma is not present in the gills of larvæ beyond 6 to 7 mm. in length. Lymphocytes (and probably erythrocytes) and the cells of the primitive thymus placodes are formed from the cells of this epithelium which does not contain a basement membrane. The cells of the epithelium have an intimate relationship to the blood channels of the gills and appear to enter into the formation of the endothelial lining when such a lining is present.

The importance of determining the character of this epithelium is obvious in the light of its relationship to lymphocyte and thymus formation. While the acceptance of an endodermal character of this tissue would lend additional proof of the endodermal origin of blood in the ammocoetes according to the researches of Goette ('90), Wheeler ('99) and Mollier ('06) and to the conten-

¹ I am greatly indebted to Mr. Peter Okkelberg of Ann Arbor, Mich., for supplying me with young developmental stages of lamprey larvae some of which were used in this investigation.

tion of various investigators that the phylogenetically oldest blood is endodermal, the character of the epithelium in the developing larva is such that one can not leave its purely endodermal character unchallenged.

The rapid change of the epithelium from a single layer of cells in the 5 mm. larva (fig. 1) to a multi-layered or massed condition in the 6 mm. larva is apparently not associated with mitotic division of the cells. In the comparatively few mitotic cells which have been observed the spindle was never so directed that the daughter cells would form a stratified epithelium.

In seeking an explanation of the increase in thickness of this epithelium one specimen measuring 5 mm. in length was found which displayed an apparent mingling of mesenchyma with endoderm in various parts of the branchial epithelium. Figure 5 represents a camera lucida drawing of one of these regions. In the lower right-hand part of the figure the endoderm is present as a single layer of cells sharply marked off from the underlying mesenchyma by a basement membrane. Above this portion the basement membrane is missing and the mesenchymal cells appear to be mingling with the endodermal cells. In the upper left-hand part of the figure a basement membrane is again present. The basement membrane in the upper part of the figure lies next to developing muscle cells; in the lower part of the figure mesenchymal cells are present between the developing muscle cells and the basement membrane.

A transverse section of the branchial region of a 5 mm. larva would show a more or less irregular outline of the endodermal lining. The gill arches are just beginning to form in this stage of development with a consequent complication of the endodermal lining. The question arises whether this apparent mingling of the two tissues as represented in figure 5 is not an artifact, the result of a tangential section through a part of the specimen. A reconstruction of a few sections of this region was made in the hope of determining this point. The reconstruction demonstrated that the epithelium is cut tangentially at this place, but it also shows a tangential plane of section in other parts of the branchial epithelium where the basement membrane is distinctly

visible. The degree of deviation of the section from the transverse plane is not any greater at the point of apparent mingling than it is in some other parts of the section where the basement membrane is visible. The angle of the plane of the section in relation to the plane of the basement membrane does not satisfy an explanation of the absence of the basement membrane at the apparent point of mingling.

The apparent mingling of the two tissues is further suggested in the character of the branchial epithelium in later developmental stages.

Figure 7 represents a frontal section through the entire gill and gill arch of a 6 mm. larva. In this stage of development the primitive gill pouches have enlarged producing an approximation of the two hemibranchs in the formation of the gill septa. The constriction at the left of the figure represents the point of attachment of the branchial septum to the lateral wall. The primary gill lamellae are in the early stages of formation, indicated at *gl.* 1 and 2 in the figure. It is evident from an examination of the figure that a single layered-epithelium is not present in the greater part of the section. The cells form a continuous mass from the exterior to the interior. In places, for example *end* in the figure, the single layered condition still persists. This patch may represent one of the patches which in later developmental stages contains cilia.

A single section as represented in figure 7 may be misleading when considered alone and apart from the sections preceding and following. The apparent continuity of the cells from the exterior to the interior may be due in part to the folding of the epithelium in the formation of the gill lamellae. However, this is not true of all parts of the section for the continuity of the massed condition of the cells in some places will persist through a number of sections.

Figure 6 represents a camera lucida drawing of a frontal section through a gill arch and a part of the gill septum of a 9.5 mm. larva. In this stage of development the cells are approaching the stage at which they transform into lymphocytes. At the surface of the part which represents a gill arch a layer of thin cells have formed (*s.c.* fig. 6). Such a layer of cells in this situation is appar-

ently in the process of formation in the younger larva as represented in figure 8 (longitudinal section through a gill arch of a 7.5 mm. larva). The cell at X in the figure appears as if it were migrating from the deeper part of the cell mass in the formation of the surface or cuticular layer.

In the growth of the larva the mass of cells is gradually depleted so that in the full-grown larvae the secondary lamellae contain only a layer of thin cells lying next to the blood channels. The massed condition of cells is retained longest in the angles between the secondary lamellae.

A product of this epithelium which, it seems to me, demands more than a passing interest are the cells represented at *d.c.* in figures 3 and 4. So far as I can learn this type of cell was first described by Graf von Spee ('96). More recently the cell has been encountered in the blood work of Stockard ('15), Emmel ('16) and others. Stockard considers these cells of a 'questionably degenerate type' while Emmel speaks of them as 'phagocytic inclusions.' In the lamprey larva these cells are especially numerous in the branchial epithelium of the 15 mm. stage. While an occasional one may be found in slightly younger and older stages the branchial epithelium of the 15 mm. larva is literally filled with these cells. There is apparently a limitation of this process to a definite developmental stage.

The cells in question appear to form as a final product of a breaking down process as represented at *e.d.* in figure 3. This figure illustrates only one step of the process. The next step is a vacuolization of the entire cell and the gathering together of the chromatin and the cytoplasmic remains into a cell-like body within the hollow original cell. These cells are very characteristic in appearance. The cytoplasm has a homogeneous structure and with eosin stains a deep pink. The chromatin material is generally present as a single globular body, very compact and darkly stained. The chromatin may be represented by a number of such bodies, however, and sometimes they stain a very pale blue.

What is the significance of the formation of this apparently degenerate type of cell? The answer to this question can, of necessity, only be made in the nature of hypothesis.

In the consideration of these cells the results of Shipley's ('16) work on the development of erythrocytes *in vitro* is suggestive. Shipley found that some of the erythrocytes in the culture developed into cells with pyknotic nuclei and suggests that the strange environment may be the cause of the degeneration. So far as I can judge the cells that Shipley describes resemble very closely the apparently degenerate cells found in the branchial epithelium of the lamprey larva.

Is it probable that the degenerate cells in the branchial epithelium of the lamprey larva are cells which have become lodged in an unfavorable environment? In support of such a possibility there is a type of cell found in this epithelium which has the appearance of erythrocytes. Such cells are represented at *ery* in figure 2. These cells have a more or less vesicular nucleus and the cytoplasm is not so homogenous as in the degenerate type of cell. The nucleus is not as vesicular, however, as it is in the developing erythrocytes in other parts of the body. These erythrocyte-like cells are apparently formed in this epithelial mass. It is, however, quite impossible to say with certainty that they are formed here, for vascular channels are forming in the mass of cells simultaneously. From this consideration it might be suggested that cells with erythrocyte potentialities are present in the branchial epithelial cell mass; that some of these cells have environments approximating the conditions which are essential for erythrocyte development while others are apparently in an unfavorable environment and degenerate.

Another possibility suggests itself in the explanation of these cells. Their formation in connection with hematopoietic anlagen (not only in the lamprey, but also in other forms where they have been described) may be essential to blood formation. They may possibly have chemotactic properties in the nature of hormones serving as a stimulus to blood formation.

The evidence submitted in the foregoing pages, it seems to me, warrants a conclusion that the branchial epithelium of the advanced lamprey larva is a compound tissue composed of endoderm

and mesenchyma. While the one specimen represented in figure 5 may possibly be an artifact, the character of the epithelium in the older larvae suggests a mingling of the two tissues. Such a mingling of tissues, however, is not a newly discovered histogenetic process. In the development of the thymus in higher animals mesenchymal and endodermal cells mingle in the formation of the organ. The process in higher animals is fundamentally the same as it is in the lamprey larva, but it differs in the amount of the tissue involved. In the thymus formation of higher animals the mingling is limited to localized areas; the mingling of the tissues in the lamprey larva occurs throughout the general branchial epithelium.

Such a tissue mingling is obviously a normal process so far as the thymus is concerned in the lamprey larva. It is only a small part of the entire epithelium, however, that enters into thymus formation. The cells of the greater portion of this mixed tissue are transformed into lymphocytes.

With the staining methods that I have employed it has been impossible to follow the further history of either tissue as an individual element in the mixed tissue. The cells appear to be all alike, i.e. in the early indifferent stage. It is consequently impossible at this time to determine whether the lymphocytes are formed from the endodermal element or the mesenchymal element or the product of the two tissues combined.

The formation of a thin cuticular layer at the surface of the mass of cells in the developing larva is likewise difficult of explanation. The cells forming this layer were earlier a part of the general mass of cells.

The outstanding feature of this mingling or fusion process is the indicated histogenetic relationship of lymphocyte formation (and probably erythrocyte formation) to thymus formation in this primitive animal. While the thymus in higher animals has retained the process of endodermal and mesenchymal fusion or mingling as essential to the formation of the organ, lymphocyte formation in higher animals has apparently dispensed with the endoderm.

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PLATE 1

EXPLANATION OF FIGURES

1 Frontal section of gill of a 5 mm. larva. *b.a.*, blood vessel; *end.*, endoderm; *mes.*, mesenchyma; *v.c.*, endothelial cells (?). ($\frac{1}{12}$ oil immersion obj., comp. oc. No. 12.)

2 Small portion of the branchial epithelium of a 15 mm. larva. *ery.*, young erythrocytes (?). ($\frac{1}{12}$ oil immer. obj., comp. oc. No. 12 $\times$ 2.)

3 Portion of branchial epithelium of 15 mm. larva. *d.c.* degenerate cell; *e.d.*, cell in which the degeneration process has just begun. ($\frac{1}{12}$ oil immersion. obj., comp. oc. No. 12 $\times$ 2.)

4 Portion of the branchial epithelium of a 15 mm. larva. *d.c.*, degenerate type of cell, lower one apparently in a young blood vessel. ($\frac{1}{12}$ oil immer. obj., comp. oc. No. 12 $\times$ 2.)

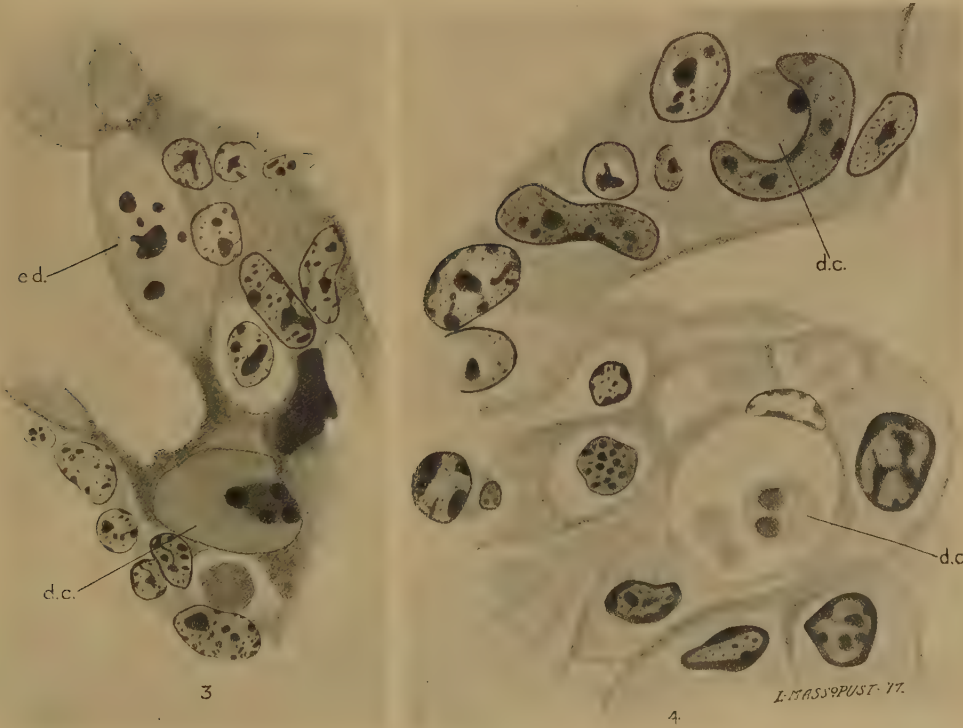
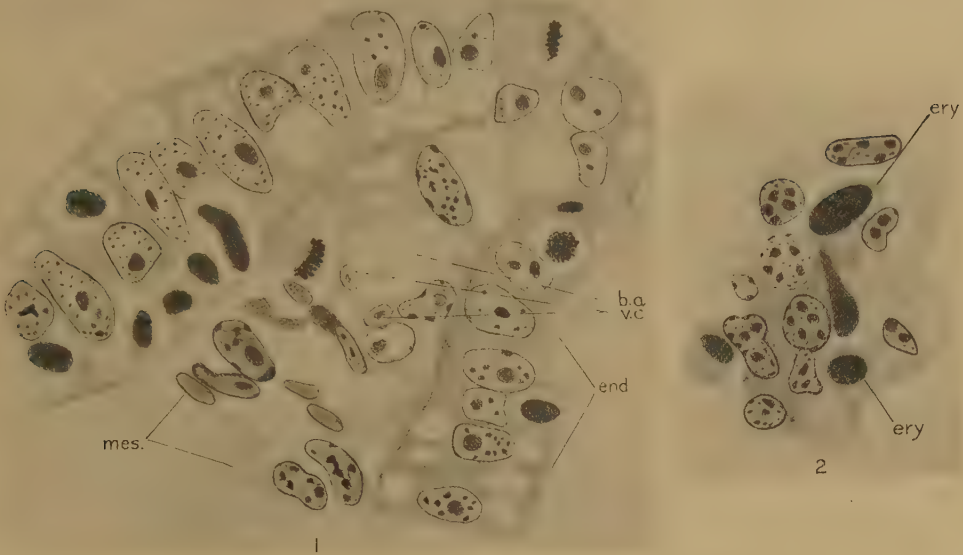


PLATE 2

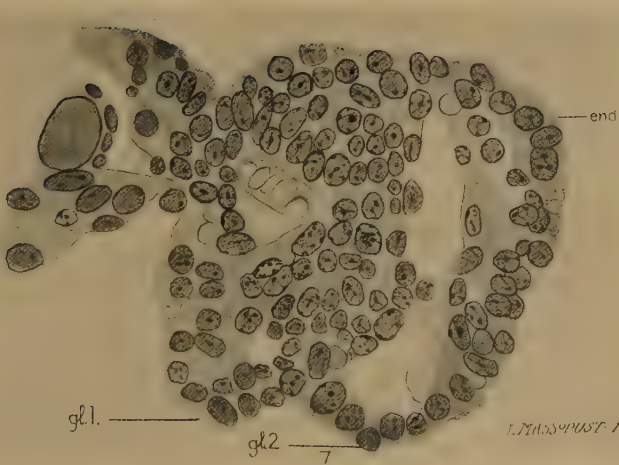
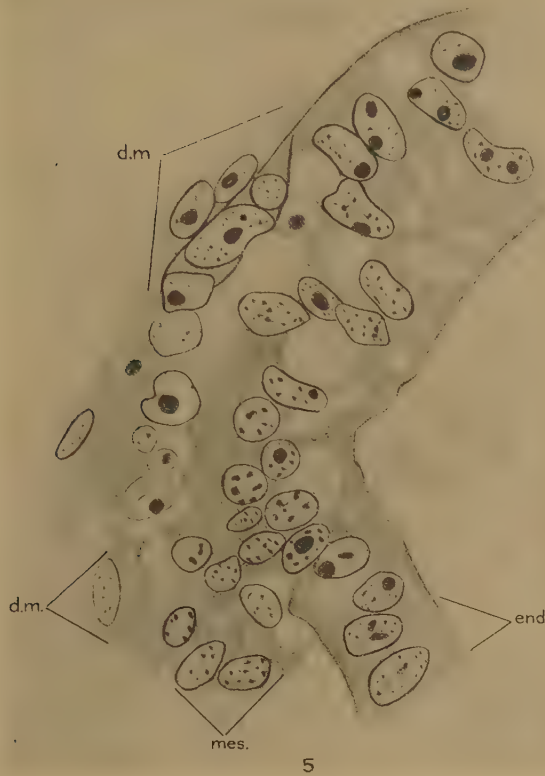
EXPLANATION OF FIGURES

5 Part of a transverse section of the branchial region of a 5 mm. larva. *dm.*, developing muscle cells; *end.*, endoderm; *mes.*, mesenchyma. ($\frac{1}{2}$ oil immer. obj., comp. oc. No. 12.)

6 Frontal section of gill arch and part of gill $\frac{1}{2}$ septum of a 9.5 mm. larva. *b.a.*, blood vessel containing erythrocytes; *s.c.*, surface or cuticular layer of cells. ($\frac{1}{2}$ oil immer. obj., oc. No. 10.)

7 Frontal section of gill of a 6 mm. larva, *end.*, patch of cells which still retain endodermal characters; *gl.1* and *2*, gill lamellae in process of formation. ($\frac{1}{2}$ oil immer. obj., oc. No. 10.)

8 Longitudinal section through a gill arch of a 7.5 mm. larva. *en.*, endothelium of blood vessel; *x*, cell which appears to be migrating from deeper part to the surface. ($\frac{1}{2}$ oil immer. obj., comp. oc. No. 12.)



ON THE ANLAGE AND MORPHOGENESIS OF THE
CHORDA DORSALIS IN MAMMALIA, IN PARTICULAR THE GUINEA PIG (*CAVIA COBAYA*)

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FOURTEEN FIGURES

The discussion here undertaken is one which is in no sense foreign to anatomic and morphologic literature; indeed it may be stated that there is perhaps no single subject in vertebrate embryology which has been so frequently and so ably investigated and has formed the basis of such extensive and fundamental speculation, as the subject here under consideration. The discussion of the anlage of the mammalian chorda dorsalis, involves a consideration of the anlage and homologies of the primary germ layers, the question of blastulation and gastrulation, considered ontogenetically and phylogenetically; in a word, the consideration of the embryologic stages immediately following the stages of segmentation. A full consideration of this broad question is beyond the limits of this communication. Neither is it possible to consider here at all completely the extensive literature involved. This seems the less necessary since relatively recently a goodly number of investigators have given extensive and critical reviews of the literature dealing with this question as may be learned on study of certain of the contributions of O. Hertwig, Keibel, Van Beneden, Bonnet, Rabl, Hubrecht and others. I shall, therefore at the outset, limit the scope of this communication by stating that it is the purpose at this time to present observations dealing with the anlage of the mesoderm and chorda dorsalis as noted in the guinea pig, a form especially adapted for the investigation of these problems; as may be learned from the studies of Carius, Liederckühn,

Keibel, Graf Spee and others, documenting these observations by a series of figures, showing successive stages of development, taken from cross-cut and sagittal series, and to dispense very largely with a consideration of the enticing problems of blastulation and gastrulation as concerns the mammalian ovum, problems and questions which have influenced very greatly the interpretations given by certain investigators to the actual observations as recorded by them. Only a small portion of the literature reviewed, and more especially that relating to mammalia, shall here receive notice, and only as the successive stages discussed by me are given special consideration.

MATERIAL AND METHODS

The embryological material on which this investigation is based consists of many uninterrupted series, cut in the cross and in the sagittal plane, of developmental stages of the guinea pig, ranging from about the 10th day to the 15th day of development. The material is all of it 'timed'; the ages given extending from time of observed insemination to the time of killing. For fixation I have used almost wholly Carnoy's fluid. After fixation and embedding in paraffine, the sections were cut either by means of the Minot rotary microtome or on a sliding microtome with the aid of the water-on-the-knife method. The sections of the great majority of the series have a thickness of either 5 μ or of 7 μ ; some few a thickness of 10 μ . After sectioning, the series were fixed to slides by means of the water-albumen method and stained on the slide by means of hemalum and Congo-red. Every embryologist of experience knows that so-called 'timed' embryologic material of mammalia does not insure succession of stages; however, I believe all will agree that a much more complete series of stages is assured by this method, than when a chance collection is made. My own series though fairly complete lacks preparations covering as completely as might be desired certain stages of development, while other critical stages are covered by an abundance of material. The figures here presented were all drawn at relatively high magnifi-

cation, with the aid of the camera lucida, and greatly reduced in reproduction. It has seemed to me desirable to present, so far as the size of the preparation permits, for each stage, figures showing cross and sagittal sections of the entire germ disc. A comparison of successive stages is thus greatly facilitated, and it is hoped extensive description obviated. Certain of the germ discs here considered have been reconstructed by Doctor Worcester, Miss Helen L. B. Gage and myself for another study now in progress. These reconstructions have been of great aid in determining respective stages and in determining the relations and relative size of the structures primarily under consideration.

TWO LAYERED GERM DISC OF GUINEA PIG AND ANLAGE OF THE MESODERM

As is well known, the guinea pig belongs to that type of rodents presenting an inversion of germ layers. The phenomenon of segmentation and implantation of the ovum of the guinea pig have been carefully studied by Graf Spee; the question of the inversion of the germ layers, as concerns the guinea pig, by Selenka. From Selenka's account, which concerns us here most particularly, it is learned that the early stages of the blastocyst formation are not unlike similar stages as described by me for the albino rat. It is further learned that for the guinea pig, after the formation of a blastocyst with ectodermal node, visceral layer of entoderm, parietal or transitory ectoderm and ectoplacental cone, a stage corresponding in many respects to a 6 day, 16 hour stage of the albino rat (Huber, fig. 24), the further steps in the inversion differ somewhat from that observed in the albino rat. In the latter the egg cylinder elongates through growth of the extra-embryonic ectoderm, resulting in a solid egg cylinder in which a proamniotic cavity develops secondarily; while in the guinea pig the ectodermal node separates early from its close relation to the base of the ectoplacental cone and there is developed an interamniotic space separating tr ger-ectoderm and ectodermal node, and bounded on the sides by a layer of visceral entoderm. The guinea pig egg cylinder thus

elongates rapidly. It encloses in its free end, which is the antimesometrial end, a solid nodule of cells, which is here known as the ectodermal node, surrounded almost completely by visceral entoderm, which layer extends to the base of the tr ager, enclosing the interamniotic cavity. Such as are not familiar with the egg cylinder of the guinea pig of this stage of development I would refer to figure 13, plate XII, of Selenka's studies, copied as figure 590 by O. Hertwig. In the series of figures given



Fig. 1 A to E. A, 10 days, 18 hours stage of egg cylinder of the guinea pig with ectodermal node showing the very beginning of the amniotic cavity; B, 10 days, 18 hours stage, with ectodermal vesicle with small amniotic cavity; C, 11 days, 18 hours stage, with ectodermal vesicle and amniotic cavity; D, 11 days, 18 hours stage, with differentiation of wall of ectodermal vesicle into primary embryonic ectoderm and amniotic ectoderm; E, 10 days, 18 hours stage, final bilaminar stage. $\times 200$. *ent.*, entoderm; *em.ect.*, embryonic ectoderm; *am.c.*, amniotic cavity; *am.ect.*, amniotic ectoderm.

by me (fig. 1, A to E) covering the ectodermal node and vesicle stages, only the antimesometrial end of the egg cylinder is figured. The relations of the portion of the egg cylinder here figured to the entire egg cylinder of the respective stage, may readily be ascertained by comparing this series of figures with those given by Selenka, to which reference has been made.

In figure 1, A to E, are presented a series of developmental stages of the guinea pig, giving in close sequence successive stages in the development of the ectodermal node and ectodermal vesicle with closed amniotic cavity and with embryonic and amniotic ectoderm differentiated. In A, of figure 1—10 day, 18 hour stage—the entoderm, *ent.*, is found in a single layer almost completely surrounding a nodule consisting of radially arranged cells, the ectodermal nodule, presenting the very beginning of a central cavity. Only in one section of this series was this cavity clearly defined. It represents the anlage of a closed amniotic cavity. This ectodermal nodule occupies the antimesometrial end of the entodermal egg cylinder, much as a marble might occupy the end of the finger of a glove. The space beneath the ectodermal nodule and between the entodermal layer, so far as sketched, in this and in the following four figures of this series, is the interamniotic space, not especially labelled here. Figure 1, B—10 day, 18 hour stage—and figure 1, C—11 day, 18 hour stage—follow in close succession of stages, presenting successively a slightly larger amniotic cavity. In figure 1, D—11 day, 18 hour stage—a slight advance in morphogenesis may be observed. The increase in the size of the amniotic cavity is to be noted, more especially the differentiation in the wall of the ectodermal vesicle. That portion of the ectodermal vesicle which is in apposition with the entoderm, presents an ectoderm composed of tall columnar cells with nuclei in several strata, and is recognized as the ectoderm of the embryonic disc, *em.ect.*; while that portion of the wall of the ectodermal vesicle which separates the amniotic from the interamniotic cavity, consists of relatively thick, flattened cells with nuclei in one layer and is recognized as the amniotic ectoderm, *am.ect.* The embryonic ectoderm has the form of an inverted watch crystal, and is throughout in close relation to the visceral entoderm. In figure 1, E, there is presented the 23d of a series of 50 sections, having a thickness of 5 μ , passing through the antimesometrial end of an egg cylinder of the guinea pig of a 10 day, 18 hour stage. This series appears to me to represent cross sections of the embryonic disc, though I am unable to as-

certain with any degree of certainty any definite bilateral symmetry. This stage is readily deduced from the preceding one. The larger amniotic cavity is evident. The embryonic ectoderm forms a thick layer, with nuclei arranged in four to five strata, becoming abruptly thinner as the amniotic ectoderm is reached, which consists of a single layer of thick flattened cells. The embryonic ectoderm is throughout in close relation with the layer of visceral entoderm. This stage may be regarded as presenting the final stage of the bilamellar condition of the germ disc of the guinea pig, the area forming a cup-or-saucer-shaped structure with concavity toward the ectoderm. There is at this stage no trace of mesoderm, ectoderm and entoderm being throughout in close relation.

As concerns the anlage of the mesoderm in the germ disc of the guinea pig, my own series do not give an answer which is not open to question in that none of the germ discs sectioned by me, covering the stages immediately following the bilamellar stage, present the very beginning of mesoderm differentiation. The several germ discs of my series, covering this stage, though ranging over a day in difference of ages, all present a stage of mesoderm development which I can not regard as showing the first appearance of the mesoderm. I am led to believe that the anlage and early spread of the mesoderm in the germ disc of the guinea pig, occupies only a very brief period of time and that it would seem necessary to collect a large series of stages, from the end of the 11th to the beginning of the 12th day of development, to chance on the desired preparations. In the material of the white rat, covering the period of the anlage of the mesoderm, I was more fortunate, in that a number of my preparations cover this stage very satisfactorily. In figures 31 and 32 (Huber) the anlage of the mesoderm in the albino rat is shown in a stage which is slightly younger than the youngest stage showing mesoderm in my guinea pig series. The question of the anlage of the mesoderm in the albino rat was only incidentally touched upon in that publication and will be discussed more fully in a forthcoming monograph in which the development of the albino rat from the 10th to the 12th day will be considered. In

the albino rat, as I have stated on a former occasion, "The anlage of the mesoderm is from the sagittal portion of the caudal region of the primary embryonic ectoderm, the caudal part of the future primitive streak." This statement, in so far as my own series enable me to reach conclusions, is equally applicable to the germ disc of the guinea pig. In figure 2, there is pre-

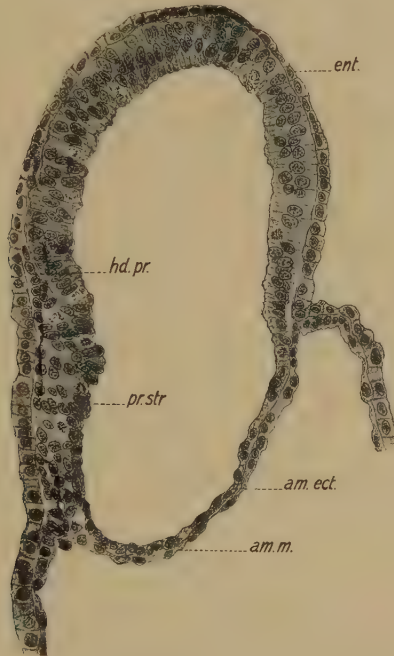


Fig. 2 Germ disc and amniotic vesicle of guinea pig, 12 days and 12 hours after insemination; early stage of mesoderm formation; anlage of head process. $\times 200$. *ent.*, entoderm; *hd. pr.*, head process, in anlage; *pr. str.*, primitive streak, in anlage with formation of mesoderm; *am. ect.*, amniotic ectoderm; *am. m.*, amniotic mesoderm.

sented practically the middle section of a series of 58 sections, having $5\ \mu$ thickness, and passing approximately through the sagittal plane of a germ disc and amniotic vesicle of a guinea pig of 12 day, 12 hours. Another germ disc, of 11 day and 18 hours, cut in the sagittal plane, though slightly obliquely to the mid axis shows essentially the same stage of development, and still another, having an age of 12 days and 7 hours, is in a stage

of development which is between that shown in stages D and E, of figure 1, and is distinctly younger than E, of figure 1, (10 days, 18 hours). The germ disc and amniotic vesicle shown in figure 2, is slightly compressed from right to left, as shown in this figure, due to a slight folding of the wall of the interamniotic cavity; however, this, so far as I am able to ascertain, has in no way influenced the relation of its parts, but gives this vesicle a slightly more elongated form than is normal, judging from the appearances presented by several other vesicles or germ discs of essentially the same stage, included in my series. From a study of figure 2, it may be observed that the outer layer of visceral entoderm forms a continuous layer, consisting of a single layer of short cuboidal or slightly flattened cells, distinctly separated as an uninterrupted and continuous layer over the entire extent of the primary embryonic ectoderm and continues into the entodermal layer forming the wall of the interamniotic cavity. Very few mitotic figures are observed in the entodermal layer; one is shown to the left in this figure. The primary embryonic ectoderm is relatively thinner than in the preceding stage described (E, fig. 1), showing two or three strata of nuclei, reduced to a single stratum of nuclei at its transition to the amniotic ectoderm, which latter extends as a single layer of flattened cells over the inner face of the amnion. Especial attention is drawn to the embryonic ectoderm of the future caudal region of this germ disc, the future primitive streak region, *pr.str.*, to the left of this figure. Very active mitosis is observed in this region and it will be noted that the sharp contour of the outer surface of the ectoderm is here lost. A migration of ectodermal cells is here noted, evidenced by the arrangement of the nuclei. The migrating cells constitute the primary mesodermal cells. As clearly seen in this section through the mid sagittal plane, certain of the cells derived from the ectoderm wander cephalad between the primary embryonic ectoderm and visceral entoderm, and are distinctly and easily separable, from both ectoderm and entoderm. This group or process of cells, derived from the ectoderm, is regarded as the anlage of the head process. If the series of sections is traced in both directions from

the mid sagittal section drawn in figure 2, it will be noted that the primary mesodermal cells have spread out on both sides of the mid axis to a little over half the circumference of this vesicle. The future head region and to the extent of about half of the spread of the primary embryonic ectoderm, is at this stage still free from the invasion of the mesodermal cells. The mesoderm of the germ disc of the guinea pig, as this series seems to indicate, though a slightly younger stage would perhaps present more conclusive evidence, has its anlage in the sagittal portion of the primary embryonic ectoderm and is clearly a derivative of the primary embryonic ectoderm of this region. The rapid spread of the mesoderm over the interamniotic cavity face of the amniotic ectoderm, is clearly shown in these preparations. In this vesicle the entire amnion consists of two layers of cells, one amniotic ectoderm, the other mesoderm, both in single layer. That the spread of the mesoderm over the amniotic ectoderm is from the caudal region of the germ disc is perhaps evidenced by the fact that the cephalic end of the germ disc is as yet free from mesoderm, see to the right of figure 2. The mesoderm extends also along the inner face of the entoderm bounding the interamniotic cavity, to approximately half the length of this cavity. There is no indication that the entoderm bounding the interamniotic space contributes to the formation of the mesoderm. At this stage, the mesodermal cells of the interamniotic space are in a single layer.

On comparison of my own account of the anlage of the germ disc of the guinea pig with that given by Selenka, it will be observed that the two accounts differ very materially. Selenka's account of the anlage of the primitive groove reads as follows:

Was zunächst die Primitivrinne selbst anbelangt, so tritt dieselbe aus als napfartige, randständige Aussackung der Ektodermblase; sie wächst sodann zu einem langen und breiten abgeplatteten Blindsacke aus, welcher sich an der Wand des Entodermmantels hinabzieht. Sehr bald verkürzt sich dieser Blindsack, dessen Lumen der Primitivrinne der übrigen Amnioten entspricht, um am 13. Tage, also etwa zwei Tage nach seiner Entstehung, sich wieder zu einer napfförmigen Grube zu verkürzen und bald darauf gänzlich zu verstreichen.

Noch ehe die blindsackförmige "Primitivrinne" ihre maximale Grösse erreicht hat, beginnt die Bildung des Mesoderms. Ihrer gan-

zen Länge nach treten aus dem dem Entodermmantel zunächst gelegenen Theile ihrer Wandung vereinzelte Mesodermzellen aus, von denen etliche, in meinen Präparaten mit Ausläufern versehene, in der Richtung nach der Basis des Keimcylinders zu sich fortschieben, während vereinzelte andere rechts und links an der Innenseite des Entoderms fortwandern, wie ich aus Quer- und Längsschnitten mit genügender Sicherheit erschliesse.

It is possible that I have missed this transitory outpocketing of the amniotic cavity which gives rise to the primitive groove and the primary mesoderm. However, in the stage described in figure 2, no distinct primitive groove is as yet recognizable, the primitive groove developing at a much later stage. The region of the primitive streak I have recognized in the stage described. It is possible that Selenka was led astray by reason of limited material, and has interpreted an artefact, due to folding of the vesicle, as a structure of consequence. Selenka's figures are difficult to judge critically in that they all appear to be more or less diagrammatic. Figure 20, plate XIII, for instance, may represent a stage which is comparable to that given in my own figure 2, however, in Selenka's figure there is no indication of the participation of the ectoderm of the caudal region in mesoderm formation; no anlage of head process and the cephalic end (?) of the embryonic disc is well invaded by mesoderm. This figure of Selenka's suggests that he has drawn a frontal section of this stage as a sagittal section, viewed in this light, it becomes intelligible. Neither Lieberkühn nor Keibel consider especially stages of the development of the mesoderm in the guinea pig of as early a stage as shown in figure 2.

A study of the literature, comprising both original sources and the more recent comprehensive reviews, reveals the fact that the majority of the more recent observers are agreed, so far as concerns mammalia, in regarding the mesoderm as a derivative of the embryonic ectoderm. O. Hertwig after discussing this question very fully in his account of the germ layers, expresses himself as follows:

Hinsichtlich des Ursprunges des mittleren Keimblattes bei den Säugetieren stimmens jetzt wohl, von einzelnen Ausnahmen abgesehen, alle Beobachter der Darstellung bei, welche zuerst Kölliker gegeben

hat. Danach ist die Bildungsstätte des mittleren Keimblattes, wie bei den Vögeln, einzig und allein der Hensen'sche Knoten, der Primitivstreifen und der Caudalwulst, also der Bezirk, in dessen Bereich ein Zusammenhang mit dem äusseren Keimblatt stattfindet und, wie leicht festzustellen ist, sich auch zahlreiche Teilungsfiguren nachweisen lassen, welche ein Rückschluss auf eine sehr lebhaft Zellvermehrung an diesem Orte zulassen.

My own views concerning this question are expressed in one of the summaries found in Keibel's article on the development of the pig. This reads as follows and summarizes my own observations on the origin of the mesoderm in the guinea pig:

“Eine andere Quelle des Mesoderms als der Primitivstreifen liess sich beim Schweine nicht nachweisen; von einem peripheren Mesoblastkeim konnten trotz genauer Nachforschung keine Spuren entdeckt werden.”

For stages following the stage showing the anlage and early spread of the mesoderm, my own material is very complete; the series at hand showing successive stages of development ranging at relatively close intervals. For the special discussion of a stage closely following that shown in figure 2, we shall consider two germ discs taken from the same uterine horn 13 days, 1 hour after insemination, and presenting almost identical stage of development. Four other germ discs, taken from the same uterus, 12 days, 16 hours after insemination, two cut in cross sections and two in the sagittal plane, are of essentially the same stage of development. The germ discs to be considered now, are only a few hours older than that described in connection with figure 2. It is necessary to call attention to the fact, that in the figures following it was deemed desirable to give the respective figures such position as would bring the entodermal layer on the under side, with amnion and ectoderm above, thus in a sense inverting the figures when compared with those shown in figures 1 and 2, and when thought of as in normal position at the antimesometrial end of a large, broad egg cylinder. In the egg cylinder as found in place in the uterus, the tr ager or ectoplacental cone is directed toward the mesometrial border, while the germ disc or embryonic area, which has the form of a porcelain evaporating dish, capping the egg cylinder, is directed

toward the antimesometrial border of the uterine tube, with the visceral entoderm as its outer layer. The diagrammatic figures of Selenka (figs. 22 to 25, plate XIII) may serve to make this clear. In figure 3, A to D, are presented drawings of a number of cross sections, taken through the antimesometrial end of an egg cylinder of the guinea pig removed 13 days, 1 hour after insemination. The series includes 90 sections of $7\ \mu$ thickness, in which the germ disc is included. This germ disc or embryonic area has the form of an inverted porcelain evaporating dish. Approximately the first twenty and the last twenty sections of the series, including the embryonic area, do not present cross, but tangential sections of the epithelial layers of the area. However, their interpretation presents no special difficulty, especially when studied under the mon-objective binocular, which I have found of great service in determining relations. This embryonic area presents a shallow primitive groove which extends about half the length of the area, the anlage of a head process, with mesoderm well developed in the caudal half of the embryonic area, and cephalad along the borders of the area, but presents a mesoderm free portion cephalad to the head process. This the following series of drawings may serve to make clear. In A (fig. 3) is presented the 16th section, counting from the cephalic border of the embryonic area. It will be noted that the entoderm under nearly the entire extent of the embryonic ectoderm is present in single layer of flattened cells, these becoming gradually taller as the interamniotic cavity is approached. The amnion consists of two layers of cells; a layer of flattened amniotic ectodermal cells and a layer of mesodermal cells. The embryonic ectoderm, to very near the border of attachment of the amnion, presents a relatively thick stratum of cells with nuclei in perhaps four layers and is bounded on its outer or under surface by a distinct *membrana prima* or basement membrane, uninterrupted through its entire extent. No mesodermal cells are to be observed between the ectoderm and entoderm throughout the greater extent of the section. The mesoderm has invaded the area for a short distance along its borders; along the attachment of the amnion. That these mesodermal wings



Fig. 3 A to D, from cross sections of germ disc of guinea pig removed 13 days and 1 hour after insemination. The entire series includes 90 sections of $7\ \mu$ thickness. A, 16th section; B, 30th section; C, 39th section; D, 49th section. $\times 100$. *em.ect.*, embryonic ectoderm; *ent.*, entoderm; *m.*, mesoderm; *hd.pr.*, head process; *pr.n.*, primitive node.

are not developed *in situ* is perhaps evident from their relation to the ectoderm and entoderm, and may be deduced from the fairly active mitosis noted in the mesodermal cells. On tracing the sections toward the caudal portion of this area, these lateral wings of mesoderm are traceable to the mesoderm of the primitive streak region. As the series is followed caudalward, two cells are observed in the axial portion of the embryonic area, between ectoderm and entoderm in the 28th section, and in B (fig. 3) is presented a drawing of the 30th section of the area. This differs from that shown in A, of this figure, in that there is observed a distinct band of cells in the axial portion of the area, situated between ectoderm and entoderm. This band of cells is readily separable from both ectoderm and entoderm, but is continuous with the cells constituting the head process and is here regarded as forming the most cephalad portion of the head process. To each side of this band of head process cells are found a few scattered mesodermal cells; a continuous layer of mesoderm being observed only near the borders of the embryonic area. The cells derived from the ectoderm in the region of the primitive streak, it would appear, invade the cephalic portion of the embryonic area in three main streams; in the axial portion as the cells of the head process and along the borders of the embryonic area as lateral wings of mesoderm. The scattered mesodermal cells observed here and there, I would regard as sprouts of the syncytial mesoderm, cut in cross section. Tsukaguchi, who has recently given an account of the early developmental stages of the goat, gives three regions of mesoderm formation:

"1. am Schildrande, 2. am Primitivstreifen, 3. höchst wahrscheinlich im mittleren Schildbezirk zerstreut."

The section here figured (B, fig. 3), seems to confirm this conclusion. We differ in the interpretation of the appearances present in our respective sections. The ectoderm and entoderm of this figure are as described in the former figure. Attention is called to the two mitotic figures found in the entoderm; one immediately under the cells of the head process. Mitotic figures in the entodermal cells are rare. There is no evidence that they contribute to mesoderm formation. C (fig. 3) reproduces a

drawing of the 39th section of this series. In the axial region of the embryonic area there may be observed a spindle shaped group of cells constituting a well developed head process. This group of cells is still distinctly separated from the ectoderm by an unbroken membrana prima, or basement membrane, and is only in contiguity with the entoderm of this region and is as yet not in distinct continuity with the lateral wings of the mesoderm, although these now encroach on the more central portion of the embryonic area. The cells of the head process present as yet no definite grouping and mitotic figures amongst them are not infrequently met with. In the fourth section further caudalward the cells of the head process become continuous with the ectoderm in the mid sagittal plane, as may be observed on a study of D (fig. 3), which reproduces the 49th section of this series and may be regarded as passing through the center of Hensen's node or the primitive node region. In the mid axial plane region of this area the ectoderm presents unusual growth activity as evidenced by the number of the mitotic figures. The membrana prima or basement membrane is in this region absent, the cells of the head process being in direct continuity with the cells of the ectoderm. The direction of the long axis of the nuclei of this region indicates an outwandering of the ectodermal cells into the head process. The derivation of the cells of the head process from the ectodermal cells of the cephalic portion of the primitive streak region, the region known as Hensen's node or primitive node is thus evidenced. It will be noted that there is here no indication of an infolding of the ectoderm to form the head process, but evidence of cell migration from the under surface of the ectoderm. The cells of the head process are in this region continuous with the mesodermal cells, this continuity is attained in the 43d section of this series. A few sections more caudal than that shown in D, of this figure, a shallow primitive groove becomes evident, which extends to near the caudal border of this area. Along its entire length the mesoderm and the ectoderm are in continuity, the membrana prima becoming evident a little to each side of the primitive groove. Active participation of the ectoderm of the primitive streak region in mesoderm formation is to be noted.

In figure 4, is presented a drawing of the 40th section of a series of 87 sagittal sections, having a thickness of $7\ \mu$, passing through an embryonic area of the guinea pig 13 day, 1 hour after insemination. In this figure, the caudal end of this area is directed toward the left. This area is practically of the same stage of development as that discussed under figure 3. The plane of section was not exactly parallel with the mid sagittal plane, but very nearly so. A little study of figure 4 will enable the reader to place approximately the regions of the four cross sections drawn for figure 3; to facilitate this I have indicated their approximate position by four crosses. Especial attention

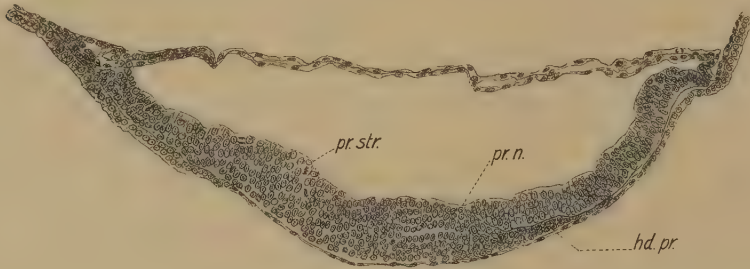


Fig. 4 The 40th section of a series of 87 sagittal sections of $7\ \mu$ thickness of an embryonic disc of the guinea pig removed 13 days and 1 hour after insemination. $\times 100$. Cephalic end of embryonic shield directed toward the right. The crosses placed beneath the figure indicate the approximate level of the sections drawn for A to D of figure 3. *pr.str.*, primitive streak region; *pr.n.*, primitive node; *hd.pr.*, head process.

is called to the head process as shown in this figure. It will be observed that the mesoderm of the caudal end—left side of figure—of this area, in the primitive streak region, is in direct continuity with the ectoderm. A little cephalad to the middle of the area, the membrana prima or basal limiting membrane, appears under the ectoderm. Just caudal to this region the cells of the head process are in direct continuity with the ectoderm of the primitive node region. The head process, thick at its caudal end, becomes gradually thinner cephalad, ultimately to be reduced to a single layer of cells. Throughout its entire extent, the head process is merely in contiguity with the ectodermal

and entodermal layers. The cephalic end of the embryonic area for a distance nearly one-fourth the length of the area, presents no cells between the ectoderm and entoderm. It will be observed that the entoderm over nearly the whole extent of the embryonic area is reduced to a single layer of flattened cells; these becoming gradually taller as the cephalic and caudal ends of the area are reached. In sections found each side of the mid sagittal plane, about 5 to 8 sections to the side of the section sketched, the mesoderm extends practically the whole length of the embryonic area and is distinctly separable from the ectoderm and entoderm. In figure 5, there is presented another section taken in the sagittal plane, showing head process. The respective embryonic area was taken from the uterus 13 days, $23\frac{1}{2}$ hours after insemination, was cut in sagittal sections of $7\ \mu$ thickness of which 126 fall to the embryonic area. The direction of the sections is not exactly parallel to the mid sagittal axis, though very nearly so. The figure reproduces a drawing of the 65th section, and presents a stage of development which is only very little older than that shown in figure 4. In figure 5, the cephalic end of the area is directed toward the bottom of the page, at the extreme top of the figure there may be observed the anlage of the allantois, just caudal to the amnion attachment, indicating a slight advance in development over that shown in figure 4. In the stage now under discussion, the primitive streak region extends more than half the length of the embryonic area, as may be clearly noted on study of figure 5; the primitive streak presenting at this stage of development its greatest relative length. My own series of guinea pig embryonic areas contains no preparation in which the primitive streak extends the entire length of the embryonic area, neither have I observed such a stage in the very complete series of albino rat embryos at my disposal, a stage which Keibel has described for the pig. I question, therefore, whether the guinea pig presents a stage in which the primitive streak extends the entire length of the embryonic area. In the stage here under discussion, a free head process is well developed and extends in the mid sagittal plane to very near the cephalic limits of the embryonic area



Fig. 5 The 65th of a series of 126 sagittal sections having a thickness of $7\ \mu$ of an embryonic shield of a guinea pig removed from the uterus 13 days and $23\frac{1}{2}$ hours after insemination. $\times 100$. The two crosses placed beneath the figure indicate the length of the head process. *Al.*, allantoic anlage; *pr.n.*, primitive node; *hd.pr.*, head process.

proper. The region of its cephalic end is indicated in the figure by a cross as is also the region of the primitive node, the two crosses being placed just below the entoderm, the region embraced between them indicating the length of the head process. In this figure, the wedge shaped mass of cells constituting the head process, is distinctly separable from both ectoderm and entoderm; from the ectoderm through a distinct limiting membrane found on its under or outer surface, from the entoderm, while in close contiguity to it, it is still not incorporated in it, the entoderm extending as an uninterrupted layer, composed of relatively thin, flattened cells along nearly the entire length of the embryonic area, in the mid sagittal region. In the region of the primitive node, which region extends through 12 sections in this series, the caudal end of the head process is in intimate relation with the ectoderm; the relatively active mitosis of the region, indicating a growth zone for the cells of the head process. Cephalad to the end of the head process there is found a small area in which at this stage the entodermal cells are slightly thicker and where ectoderm and entoderm are not separated by intervening cells. This small area I have regarded as approximately the region of the future primary pharyngeal membrane or oral plate. Cephalad to this area there may be observed in this section a few mesodermal cells. These, it would appear to me, have invaded this region from the lateral wings of mesoderm, which have by this stage grown forward along the borders of the embryonic area to reach its cephalic portion. This region is regarded as that in which the pericardial space develops. If my interpretations of relations in front of the cephalic end of the head process at this stage be accepted, it will be observed that the head process extends cephalad to approximately the region of the future primary pharyngeal membrane or, oral plate, thus obviating the necessity of postulating a 'replacement plate'—'Ergänzungsplatte'—of entodermal origin such as Bonnet has described for the dog, a structure which I have not observed in the guinea pig. A free head process, such as here described for the guinea pig has been observed in a number of mammals; by Lieberkühn, Strahl, Cariu and Keibel for the guinea pig, by

Kölliker and Rabl for the rabbit, by Keibel for the pig, by Bonnet for the sheep and dog, by Van Beneden for the bat and by Tsukaguchi for the goat. Keibel who has investigated the guinea pig with reference to the anlage of the chorda dorsalis, speaks as follows concerning the development of the head process in this form:

Vom Henschen'schen Knoten aus wächst nun cranialwärts der Kopffortsatz. Der Kopffortsatz aber liegt hier zunächst vollkommen frei zwischen Ectoblast und Entoblast, wie denn in diesem Stadium überhaupt an keiner Stelle des Meerschweincheneies ein Zusammenhang von Mesoblast und Entoblast annehmbar erscheint. Die Bilder sprechen hier so deutlich, dass man jeden Gedanken daran sofort von sich weisen kann. . . . Der Kopffortsatz ist ausschliesslich vom Mesoblast gebildet, und obwohl manche Forscher angeben, dass derselbe mit dem Entoblast innig verlöthet sei und an dieser Stelle der Entoblast wirklich mesoblastische Zellen bildet, so konnte ich mich doch nicht überzeugen, dass die platten Entoblastzellen die passive Rolle einer Bekleidung des mesoblastischen Kopffortsatzes aufgaben, um active an seinem Wachsthum sich zu betheiligen.

Keibel states here very correctly the origin and the relations of the head process, but speaks of it as developed from the mesoderm. I would consider the head process as also the mesoderm as a direct derivative of the ectoderm, a view which will receive further discussion in subsequent pages.

The stage of a free head process is followed by one in which the entoderm comes in very close relations with the under or ventral surface of this process and the under surface of the cell mass constituting the primitive node region. An actual fusion of the head process and the mesoderm of the primitive node region with the entoderm, in the sense that the caudal end of the head process and the mesoderm are fused with the ectoderm of this region, does not obtain; the entoderm extending as a continuous membrane, composed of very much flattened cells, along the axial portion of the embryonic area, readily distinguished from the overlying cells in all sections passing through this region, whether cut in the cross or sagittal planes. At this stage, the cells of the caudal end of the head process present an important rearrangement. Those dorsally placed assume a more regular arrangement and an epithelioid character and a narrow

space is differentiated beneath them; the caudal end of the head process assuming the form of a compressed column of cells, its cells presenting radial arrangement about a narrow central lumen. This differentiation leads to the formation of a structure long known as the chordal canal, which constitutes an important phase in the anlage and morphogenesis of the chorda dorsalis. In figure 6, A to D, there are reproduced a series of drawings of sections of an embryonic area of guinea pig, re-

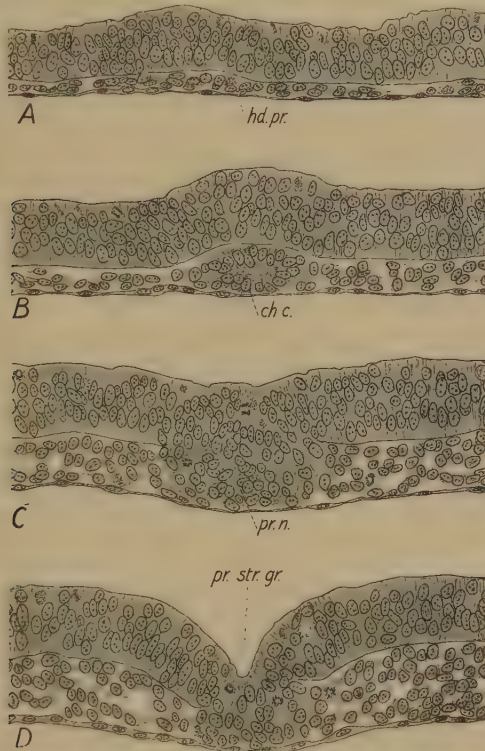


Fig. 6 A to D, from cross sections of an embryonic shield of the guinea pig, removed 13 days and 12 hours after insemination; showing early stages of chordal canal formation. The entire series embraces 160 sections having $7\ \mu$ thickness. $\times 200$. A, 35th section, through head process, B, 53rd section, through chordal canal, C, 84th section, through region of the primitive node, D, 106th section, through primitive streak and primitive groove. *hd.pr.*, head process; *ch.c.*, chordal canal; *pr.n.*, primitive node; *pr.str.gr.*, region of primitive streak and primitive groove.

moved 13 days and $11\frac{1}{2}$ hours after insemination; showing early stages in the development and differentiation of the chordal canal. This series, cut cross-wise, embraces 160 sections of $7\ \mu$ thickness, extending from amnion attachment of the cephalic border to amnion attachment at the caudal border. This embryonic area presents a very well developed primitive streak and groove, extending a little over half the length of the embryonic area as also a well developed primitive node. The mesoderm is spread over the entire extent of the embryonic area except in the region of the chordal canal and the head process and the oral plate region. In the ectoderm the medullary plate has obtained outline in approximately the cephalic half of the area. On tracing this series from the cephalic amnion attachment, it will be observed that a definite thickening of the ectoderm in the more central portion of the sections appears in the 16th section and the first trace of the cephalic end of the head process are to be noted in the 22d section. In A (fig. 6) is reproduced a drawing of the 35th section of this series. In the region through which this section passes, the head process consists of two layers of compactly arranged cells, occupying the axial region of the embryonic area, and situated between ectoderm and entoderm, readily separable from each of these layers. The mesoderm of this region approaches the borders of this plate of process cells. The entoderm extends as a continuous layer, consisting of very flat and thin cells, ventral to this plate of head process cells. In the ectoderm the medullary plate is recognized as consisting of a thickened layer of ectodermal cells, with nuclei in three strata, and bounded on its ventral surface by a distinct limiting membrane. As this series is traced caudalward the first traces of a chordal canal are to be observed in the 46th section, the head process being in this section somewhat thicker than that shown in A, of this figure, though as yet presenting the form of a flat, spindle shaped structure. In B (fig. 6) is reproduced a drawing of the 53d section of this series. In this section the cells of the head process present a distinctly radial arrangement about a small centrally placed lumen, the structure constituting a chordal canal,

not as yet distinctly separated from the bordering mesoderm, which extends as a well developed layer to the borders of the embryonic area. This section—as other sections—was drawn by aid of camera lucida at a magnification of 600; reduced in reproduction. This magnification was sufficient to enable determining clearly the relations of the structures sketched; the figure may thus serve to show that the chordal canal is at this stage distinctly separable from both ectoderm and entoderm. A distinct chordal canal is traced through 24 sections of this series. In certain of these sections the lumen appears double, again fusing to a single lumen; a phenomenon previously observed. In the 76th section, the distinct limiting membrane separating chordal canal and ectoderm disappears and the wall of the chordal canal which is directed toward the ectoderm fuses with the ectoderm the lumen of the canal, however, is still evident. The region of the well developed primitive node found in this series is shown in C (fig. 6), reproducing a drawing of the 84th section. In this primitive node region the caudal end of the chordal canal and the mesoderm are fused with the ectoderm, as this drawing clearly portrays; the mesoderm extending as a massive layer to the limits of the embryonic area. In this series it is impossible to trace the lumen of the chordal canal to the surface of the ectoderm; neither is there observed a distinct infolding of the ectoderm of this region. A slight protrusion of cells in the center of the node region is noted, though this is not as pronounced as that figured by Carius for the rabbit. In D (fig. 6) is reproduced a drawing of the 106th section of this series, inserted to show a typical section of the primitive streak and groove region as presented in this series. The relations of the mesoderm to the ectoderm of the primitive streak region is here clearly shown, the direction of the long axis of the nuclei of ectodermal cells of this region evidencing a proliferation and migration of ectodermal cells to the mesoderm.

The chordal canal is a structure well recognized in embryologic literature and has been described for a number of mammals and other amniotes. Almost immediately after its anlage, its ventral surface comes into very intimate relation with the under-

lying entoderm, though in all of the series of section of embryonic shields of the guinea pig, showing chordal canal, the entoderm extends as an uninterrupted layer of flattened cells along the ventral—entodermal—surface of the chordal canal and head process. Soon after the anlage of the chordal canal, there may be noted in its caudal portion a dehiscence along its ventral wall, including underlying entoderm, so that the chordal canal assumes the form of an inverted trough, opening into the subentodermal space. The caudal end of the chordal canal, in certain of the mammalian embryonic shields carefully studied, extends to the dorsal surface of the ectoderm in the region of the primitive node, its lumen thus extending to the amniotic cavity, forming the neurenteric canal. The metamorphosis of the head process into chordal canal and the opening of this into the entoderm is described as follows by O. Hertwig:

Der Kopffortsatz bekommt in seinem Innern eine Höhlung, die meist als Chordakanal, zuweilen auch als *Canalis neurentericus* bezeichnet wird; seine untere Wand, nach dem sie mit dem innern Keimblatt eine Verschmelzung eingegangen ist, reißt längs dieser Naht ein; dadurch wird jetzt der Chordakanal seiner Länge nach in den unter dem innern Keimblatt gelegen Raum eröffnet.

As is also noted by O. Hertwig, slight variations in the detail of formation of the chordal canal in mammalia has been observed, to the extent, that two main types are recognized. In the one type the chordal canal is relatively short, opening almost immediately after its anlage into the entoderm as observed in the rabbit, sheep and pig. In the other type the chordal canal forms a much more definite structure, extending for a relatively long distance cephalad, as in the guinea pig and the bat (*Vespertilio murinus*) and according to the recent account of Grosser, in the human embryo. Particularly in the guinea pig may there be observed a relatively long and well developed chordal canal, known to literature through the studies of Lieberkühn, Keibel and Graf Spee.

In figure 7, there is presented a drawing of the 74th section of a series of 150 sections, each of $7\ \mu$ thickness, of the embryonic area of a guinea pig removed from the uterus 13 days and 12

hours after insemination, and cut in the sagittal plane. This series was very fortunately cut, the line of sectioning being almost exactly parallel to the mid axis of the embryonic shield. The figure reproduced is drawn from a single section. The caudal end of the section reproduced is readily recognized by means of the prominent allantoic anlage and which in the figure is directed toward the top of the page. For about the upper half of the length of the figure, the section passes through the primitive groove. The region of the primitive node with shallow primitive pit is indicated by figure legend, *pr.n.* From the caudal end of the embryonic area to the region of the primitive node the ectoderm shows no definite ventral boundary, but is continuous with the mesoderm of the primitive streak region. Cephalad to the primitive node region the ectoderm is bounded on its under surface by a distinct limiting membrane. Beneath the ectoderm of this region, and in close relation to it, there may be observed a long chordal canal, cut nearly through its whole length so as to include its lumen. The extent of the chordal canal is indicated by two crosses placed in the figure just beneath the entoderm. Beneath the chordal canal, the entoderm may in places be observed as a thin cuticular layer, with nuclei here and there evident. In this preparation, the chordal canal opens into the entoderm for a short distance, as is clearly seen in the figure. The chordal canal, in this preparation, does not reach the cephalic limit of the head process, this extending for a short distance cephalad, beyond the region in which a distinct chordal canal lumen can be determined. The anterior limit of the head process is not clearly defined in the series from which figure 7 was drawn. In another embryonic shield of about the same stages of development and taken from the same uterus also cut in the sagittal plane, but not in such favorable direction, the head process can be traced fairly distinctly over a continuous layer of entoderm, to near the region of the future pharyngeal membrane, though the head process cells appear as firmly fused to the entoderm. Figure 8, which is drawn from the same series from which figure 7 was taken, reproduces a portion of the 76th section and was drawn



Fig. 7 The 74th of a series of 150 sagittal sections having a thickness of $7\ \mu$, of an embryonic shield of a guinea pig removed 13 days and 12 hours after insemination. The figure presents a long chordal canal, cut longitudinally through its lumen and just opening ventrally into entoderm. The two crosses are placed so as to indicate the length of the chordal canal. $\times 100$. *Al.*, allantoic anlage; *pr.n.*, primitive node.



Fig. 8 The 76th section of the same series from which figure 7 was drawn, embracing the region of the primitive node and caudal end of the chordal canal. $\times 200$. *Ect.*, ectoderm; *ent.*, entoderm; *ch.c.*, chordal canal, dorsal and ventral wall enclosing lumen; *pr.pt.*, primitive pit.

at a higher magnification and embraces the primitive node region and the caudal end of the chordal canal. This section, for this region, passes more nearly through the mid plane of the embryonic shield than does section 74, the basis of figure 7. A distinct primitive pit, *pr.pt.*, is to be noticed in the primitive node region. The relation of the caudal end of the chordal canal to the ectoderm of the primitive node region is to be noted; the direction of the long axis of the nuclei of the ectodermal cells evidencing a growth zone for the chordal canal in the ectoderm of this region. The distinct separation of the ectoderm from the definitive chordal canal is to be observed. The relation of the entoderm to the caudal end of the chordal canal and the ectoderm-mesoderm mass of the primitive node region, is clearly shown in this figure; the entoderm extending as an uninterrupted continuous layer, consisting of flattened cells, beneath nearly the whole extent of the region figured. An extension of the lumen of the chordal canal to the surface of the ectoderm is not observed.

In none of my series, whether sectioned in the cross or the sagittal plane have I been able to determine a patent neurenteric canal. This agrees with the observations of Lieberkühn, who states, referring to the chordal canal:

“Auch ist es mir nie gelungen eine ausmündung desselben an der Oberfläche des Ectoblast wahrzunehmen,”

Graf Spee in discussing this point describes a neurenteric cord—‘Neurenterischen Strang’—with cell nuclei radially arranged, but having no lumen, and extending obliquely from ectoderm to entoderm, however, not distinctly separated from the cells of the primitive node region. This I have observed in a number of my series, cut in cross sections.

Grosser's account of a human embryo with chordal canal, is of interest in this connection. In the human embryo in question, with probable age of 18 days, the embryonic shield measured $670\ \mu$, with well developed chordal canal, having a length of $190\ \mu$. The chordal canal was found to open into the entoderm with two openings and on to the ectoderm by means of one small opening. As has been known for some time, the human embryonic shield of the pertinent stage, presents a patent neurenteric canal, well

known through Graf Spee's description and figures of embryo *G.le.*, and other more recently described embryos, including this of Grosser. So far as I am able to judge from a study of figures, the chordal canal of the human embryo described by Grosser presents many points of similarity to that found in the embryonic shield of the guinea pig presented in figure 7, the primitive streak region, however, being distinctly longer in the guinea pig. Grosser has called attention to the resemblance of the chordal canal in human and guinea pig embryos, stating:

"Am nächsten kommen noch die Bilder, die Lieberkühn vom Meerschweinchen giebt."

Figure 7, in its main features is comparable with the well known figures given by Van Beneden, giving mid sagittal sections of embryonic shields of *Vespertilio murinus*. In the embryonic shield of this bat there is present a patent and very distinct neurenteric canal. Van Beneden described two kinds of openings of the chordal canal into the entoderm. 1. An anterior opening consisting of a broad transverse slit. 2. Several smaller openings which soon fuse to form a single longitudinally directed slit. I am in accord with Keibel, when he states, referring to the two kinds of openings of the chordal canal into entoderm:

"Bei Kaninchen erscheint mir dieselbe durchaus nicht zutreffend, und wie schon gesagt, finde ich sie auch für Meerschweinchen nicht bestätigt."

Lieberkühn was the first to call attention to the fact that the chordal canal does not open ventrally, primarily, by means of a single longitudinally directed slit, but usually by means of a series of smaller openings. This is clearly seen in his figure 30 of plate 20, giving a ventral surface view of an embryonic shield, also his figures 25 to 29 of the same plate. This fact is also clearly shown in the series of ten drawings grouped under figure 9. These drawings are from representative sections of an embryonic shield of a guinea pig removed from the uterus 13 days and 12 hours after insemination, and taken from the same uterus from which the embryonic shield, a section of which was reproduced in figure 7 was taken, though that shield is of slightly younger stage of development. The series of sections of the

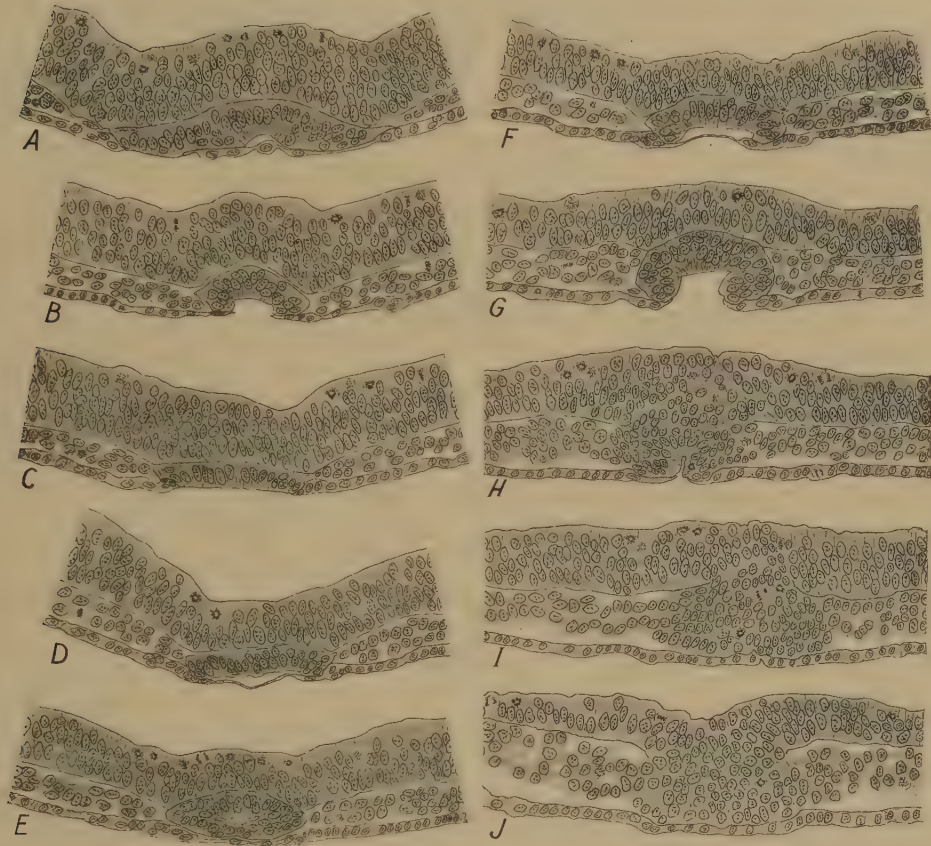


Fig. 9 A to J. Drawings of representative cross section of an embryonic shield of the guinea pig, removed 13 days and 1 hour after insemination. The series embraces 188 sections of 7μ thickness. $\times 200$. A, 33rd section, through chordal plate with entoderm extending beneath; B, 43rd section, with arched chordal plate, entoderm extending under borders of chordal plate; C, 53rd section, flattened chordal plate incorporated in entoderm; D, 66th section, with flattened chordal plate with entoderm extending beneath; F, 79th section, arched chordal plate with entoderm extending beneath; G, 107th section, arched chordal plate, entoderm extending under the borders of chordal plate; H, 114th section, chordal canal reaches into ectoderm; I, 120th section, primitive node region; J, 155th section, primitive streak region.

embryonic shield from which figure 9 is drawn, numbers 188 cross sections having a thickness of $7\ \mu$. Each of the several drawings of this figure includes the axial portion of the embryonic shield as seen in cross section, with the ectoderm of the medullary plate, the primitive node and the primitive streak directed upward and with mesoderm and entoderm in normal relations. The chordal canal or metamorphosed chordal canal structures are to be found in the middle and under side of each drawing, either as a closed chordal canal or showing various degrees of ventral dehiscence and so-called incorporation into the entoderm. A (fig. 9) is of a drawing of the 33d section, counting from the cephalad border of the embryonic shield. This section falls to the region slightly caudal to the region of the future pharyngeal membrane, a region in which it is believed a chordal canal with patent lumen does not develop, instead, the cells of the head process differentiate to form a chordal plate composed of short columnar cells, as indicated in the drawing. It will be observed that the entoderm extends beneath this chordal plate, in the drawing from right to left, for nearly the entire extent of the chordal plate. B of this series reproduces a drawing of the 43d section. In this region the chordal canal has opened ventrally, presenting in cross section the form of an inverted trough. It is further to be noted that the dehiscence extends through the entoderm, but that the edges of the entoderm extend beneath the borders of the arched chordal plate. C of this series is a drawing of the 53d section. The borders of the chordal plate are in this region spread out so as to bring the plate into a plane, seemingly incorporated between the edges of the cleft entoderm. However, by reason of the staining reaction of the protoplasm of the cells of the chordal plate and their short columnar shape, they are readily differentiated from the entodermal cells. D, of this series is of a drawing of the 66th section. In this region the chordal canal through ventral dehiscence and spreading has assumed the form of a plate, however the splitting did not involve the entoderm, this extending as a cuticular layer beneath the plate of chordal cells. E, of this series is of a drawing of the 75th section. In this region

there may be observed a very distinct chordal canal, with slit like lumen, the entoderm extending as an uninterrupted layer of flattened cells beneath the chordal canal. In F, of this series there is reproduced a drawing of the 79th section, and is of a region in which the entoderm extends as a cuticular layer beneath an arched chordal plate. G, of the series, is of a drawing of the 107th section. The region from which this section was taken approaches the primitive node region. The ventrally opened chordal canal presents in cross section the form of an arch the lips of the split entoderm extending under the borders of the arched chordal plate. Throughout this portion of this series of drawings, A to G, the chordal canal or plate is distinctly separated from the ectoderm, this presenting a definite limiting membrane on its under or ventral side. In H, of this series, reproducing a drawing of the 114th section, the chordal canal reaches into the ectoderm of the primitive node region and is no longer distinctly separated from the ectoderm, although the fusion with the ectoderm is not as yet as complete as shown in the following drawing. Ventrally the chordal canal opens into the entoderm through a narrow slit. I, of this series reproduces a drawing of the 120th section, which passes through the primitive node region. In this region the caudal extension of the chordal canal is distinctly fused with the ectoderm, the direction of the long axis of the nuclei and the active mitosis indicating an ectodermal growth zone for the chordal canal. J (fig. 9) reproduces a drawing of the 155th section, which passes through the anterior portion of the primitive streak and groove, and is added to show the active participation of the ectoderm of the primitive streak region in the formation of mesoderm. Throughout the primitive node the entoderm extends as an uninterrupted layer of cells.

This series of drawings may serve to illustrate how difficult it would be to portray adequately by means of a single illustration the dehiscence of the ventral wall of the chordal canal and its incorporation in the entoderm of the axial portion of the embryonic shield. A definite incorporation of the chordal plate into the entoderm, it would appear to me, does not obtain, and

as concerns the guinea pig, there is at hand no evidence that the entoderm in any way contributes to the histogenesis of the chordal canal or chordal plate. In corroboration of this conclusion two further series of drawings are here added: they are of cross sections of slightly older stages than that discussed under figure 9.

In figure 10, drawings A to F, there are presented a series of six drawings of cross sections of an embryonic shield of the guinea pig removed from the uterus 14 days and 11 hours after insemination. This series included 188 cross sections of $7\ \mu$ thickness. Measured as to age, reckoned from time of insemination to time of killing, this embryonic shield is nearly a day older than that discussed under figure 9. In actuality it presents only a slight advance in development; both as to general development and specifically as concerns chordal structures and their relations. Drawing A (fig. 10) is of the 30th section counting from the cephalic border of the embryonic shield, and is from the region slightly caudal to the future pharyngeal membranes. A chordal plate is here observed with the entoderm extending as an uninterrupted layer ventral to it. B, of this series is of a drawing of the 44th section. Here also the entoderm extends ventral to the chordal plate. C, of this series is of a drawing of the 57th section. In this region there is observed a slit in the entodermal layer, the edges of the split entoderm extending under the borders of the chordal plate. D, of this series reproduces a drawing of the 86th section. In this region the chordal plate is relatively wide, and as seen in cross section, of the form of a broad arch, with the edges of the separated entoderm extending under the borders of the chordal plate. E, of this series reproduces a drawing of the 107th section, which approaches the region of the primitive node. The ventrally open chordal canal presents in cross section the form of an arch, beneath which extends the entoderm as a thin but continuous layer. In the several drawings of this series, A to E, thus far considered, the ectoderm is separated from the chordal plate by a distinct, basal limiting membrane. F, of this series is of a drawing of the 119th section, which passes through the primitive node region, in

which region the caudal end of the chordal canal is continuous with the ectoderm with total disappearance of the basal limiting membrane. The active mitosis of the ectoderm and deeper cells indicate a region of growth activity. Ventrally the mesoderm is in continuity with the cells of the primitive node. The entoderm passes uninterrupted ventral to this area. In no por-

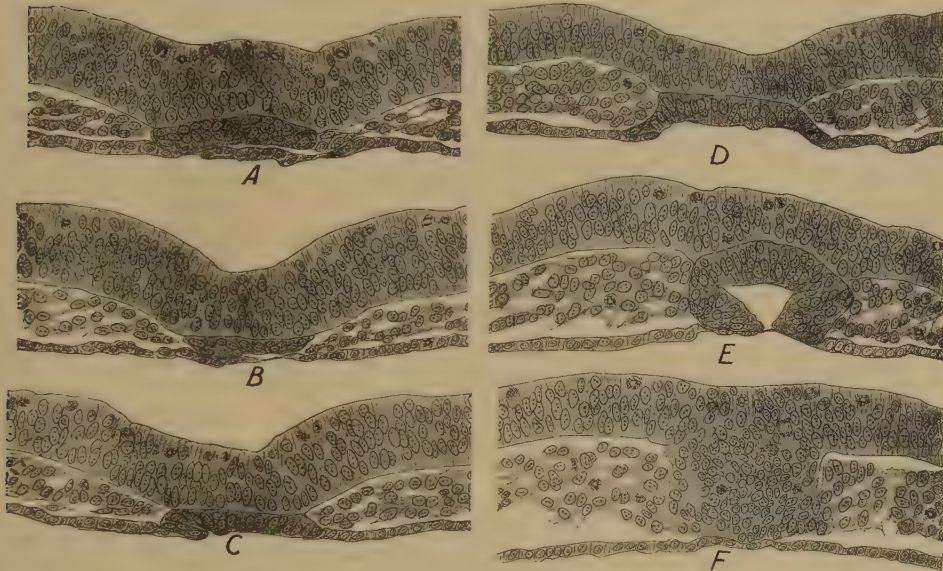


Fig. 10 A to F. Drawings of representative cross sections of embryonic shield of the guinea pig, removed 14 days and 11 hours after insemination. The series embraces 188 sections shaving 7μ thickness, and shows relations of the chordal plate. $\times 200$. A, 30th section, with flattened chordal plate with entoderm extending beneath; B, 44th section, with flattened chordal plate with entoderm extending beneath; C, 57th section, chordal plate incorporated in entoderm; D, 86th section, wide arched chordal plate incorporated in entoderm; E, 107th section distinctly arched chordal plate with entoderm extending beneath; F, 119th section, primitive node region.

tion of this series, from region of the primitive node to cephalic end of head process was there observed a closed chordal canal, though in several regions the entoderm extends beneath the chordal plate, which results from dehiscence of the ventral wall of the chordal canal. In the regions in which the entoderm presents a cleft under the chordal plate, the edges of the cleft entoderm extend slightly under the borders of the chordal plate.

In figure 11, A to F, are reproduced a series of six drawings of respective cross sections of an embryonic shield of a guinea pig removed from the uterus 14 days and 7 hours after insemination. This embryonic shield was cut in cross sections having $5\ \mu$ thickness; 327 sections fall to the embryonic shield. As measured by age this embryonic shield is slightly younger than that discussed under figure 10; as judged by stage of development, it is slightly older, as indicated in general by the presence of a well developed medullary groove in the cephalic portion of the embryonic shield. In A (fig. 11) is reproduced a drawing of the 42nd section, counting from the front part of the embryonic shield. This section passes just caudal to the forming foregut, so that the entoderm is cut slightly tangential, this accounting for its apparent thickness as seen in the figure. In this region the chordal plate is relatively wide, with the entoderm, left side of the figure, extending beneath the chordal plate. In B, of this series is reproduced a drawing of the 67th section. In this region the chordal plate is relatively narrow, with the edges of the cleft entoderm extending distinctly under the borders of the chordal plate. In C, of this series is reproduced a drawing of the 123rd section and gives a conventional figure of a flat chordal plate apparently incorporated into the entoderm, though on closer study it may be observed that the edges of the cleft entoderm extend slightly under the borders of the chordal plate. D, of this series is of a drawing of the 223d section. In this region the chordal plate is again relatively wide, appearing in cross sections slightly arched, and especially on the left side, definitely incorporated in the entoderm; the edge of the entoderm extending under the border of the chordal plate on the right side. In E, of this series there is reproduced a drawing of the 234th section; this approaching the region of the primitive node. In this section, as may be observed from the figure, the chordal plate is not completely separated from the ectoderm, but in the middle of the chordal plate, it is continuous with the ectoderm; the rather distinct radial grouping of the nuclei in the region of fusion of the chordal plate and ectoderm indicating the region of the neurenteric cord as described by Graf Spee. In F, of this series there

is reproduced a drawing of the 238th section, which passes just cephalad of the anterior border of the primitive node, and presents the caudal end of the definitive chordal canal and its extension into and fusion with the ectoderm of the primitive node

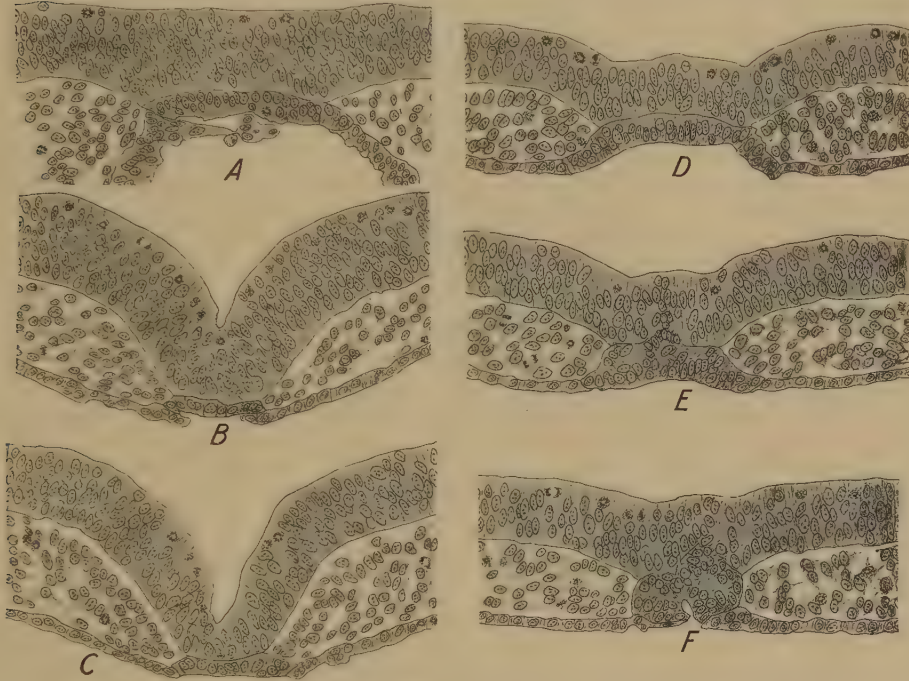


Fig. 11 A to F. Drawings of representative cross sections of an embryonic shield of the guinea pig removed 14 days and 7 hours after insemination. The entire series embraces 327 sections having 5μ thickness; neural groove in cephalic portion of embryonic shield; as yet no somites; final stage of chordal plate. $\times 200$. A, 42nd section, just caudal to foregut, chordal plate with entoderm extending beneath; B, 67th section, flattened chordal plate with entoderm extending under the borders of the chordal plate; C, 123d section, flattened chordal plate beginning to fuse with the ectoderm; D, 223d section, relatively wide and slightly arched chordal plate incorporated into the entoderm; E, 234th section, approaches primitive node region, chordal plate beginning to fuse with ectoderm; F, 238th section, just cephalad to border of primitive node.

region. The narrow ventral cleft extends through the entoderm, the edges of the cleft entoderm passing beneath the borders of the ventrally open chordal canal. Throughout this series the chordal plate is only in part incorporated in the entoderm. In figure

12, is presented a drawing of a mid sagittal section of an embryonic shield of practically the same stage of development as that discussed under figure 11. This series is of an embryonic shield of a guinea pig removed from the uterus 14 days and 12 hours after insemination, and includes 156 sections having 7μ thickness. The figure reproduces a drawing of the 79th section, and is drawn from a single section, the line of sectioning in this series being almost exactly parallel to the mid axis. The caudal end of the section is directed toward the top of the page, as evidenced by the prominent allantoic anlage. A study of the series reveals that the stage of development is that just prior to the formation of the first somite, this being indicated but not completely formed. The primitive streak region extends for a little more than a third of the length of the embryonic shield. The first indication of the pericardial space is to be noted. The chordal plate of this shield extends from the region of the primitive node, *pr.n.*, to approximately the region of the future pharyngeal membrane, and is in close relation to the ectoderm, being separated from it by the distinct basal limiting membrane of the ectoderm. Here and there entodermal cells are to be observed beneath the chordal plate. The chordal canal is still evident for a short distance at the caudal end of the chordal plate, which becomes continuous with the ectoderm of the primitive node region. At this stage the ectoderm and mesoderm are still continuous in the primitive streak region, the entoderm extending beneath this region as an uninterrupted layer. In order to reproduce in one section, reduced to page length, the entire embryonic shield in a mid sagittal section, the reduction necessary obviates a clear presentation of details. It is hoped the figure is sufficiently clear to enable orientation. It may also be stated that cross sections give clearer pictures of the relations of the chordal plate at this stage than do sagittal sections. These two series, figures 11 and 12, it may be stated, represent approximately the final stage in chordal plate morphogenesis and its incorporation into the entoderm. This stage is followed by one in which the chordal plate again separates from the entoderm and differentiates to form the definitive chordal dorsalis.



Fig. 12 The 79th of a series of 156 sagittal sections having 7μ thickness, of an embryonic shield of a guinea pig, removed 14 days and 12 hours after insemination. $\times 75$. Embryonic shield in final stage of chordal plate incorporation in entoderm; caudal end of shield directed toward the top of the page.

O. Hertwig's endeavor to find support for his 'Celometheorie' in mammalian embryonic discs with ventrally open chordal canal, it would seem to me, is not sustained. Hertwig finds support for his contention in the accounts and figures of Heape—mole, and Van Beneden—rabbit. In his discussion of these figures (figs. 618 and 619) he states:

"Links und rechts geht das Chordaepithel Kontinuierlich in das parietale Blatt des Mesoblasts über, das aus mehr abgeblateten Zellen besteht."

As my own figures may serve to show (figs. 8, 9, and 10), the mesoderm is not directly continuous with the borders of the chordal plate, from the region just cephalad of the primitive node to its anterior limits.

The separation of the chordal plate from the entoderm has been carefully studied by a number of investigators; first by Lieberkühn, in the guinea pig, later by Keibel, in the guinea pig and rabbit. Keibel formulates his conclusions as follows:

Die Chorda kann sich aus dem Verbande des Entoblasts sowohl durch einfache Unterwachsung, als durch directe Einfaltungsprozesse ausschalten. In ersteren Falle erhalten wir eine platte Chorda, wie sie Z. B. aus dem Köllikerschen Handbuch bekannt genug ist; im zweiten hat die Chorda alsbald eine Gestalt, welche ihre definitive gleich ist oder ihr doch nahe kommt. In den Fällen, in welchen die Chorda zunächst einfach aus dem Entoderm ausgeschaltet wird, erfolgt nachträglich eine Umordnung der Chordazellen, welche einem Einfaltungsvorgang gleich zu setzen ist. In beiden Fällen kann nachträglich noch ein Canal im Inneren der Chorda auftreten, welchen ich als "secundären Chorda canal" bezeichnen will.

These two methods of chordal plate separation, it seems to me, are exemplified in the figures presented in figure 13. The series forming the basis for this figure are of an embryonic shield removed from the uterus 14 days, 11 hours after insemination, and are from the same uterus from which the embryonic shield described under figure 10, was taken. The series includes 340 sections of 7μ thickness. There are present five pairs of somites with a sixth pair forming. In A (fig. 13) is reproduced a drawing of the 170th section. The line of sectioning is not quite at right angles to the mid axis, as evidenced by the difference in

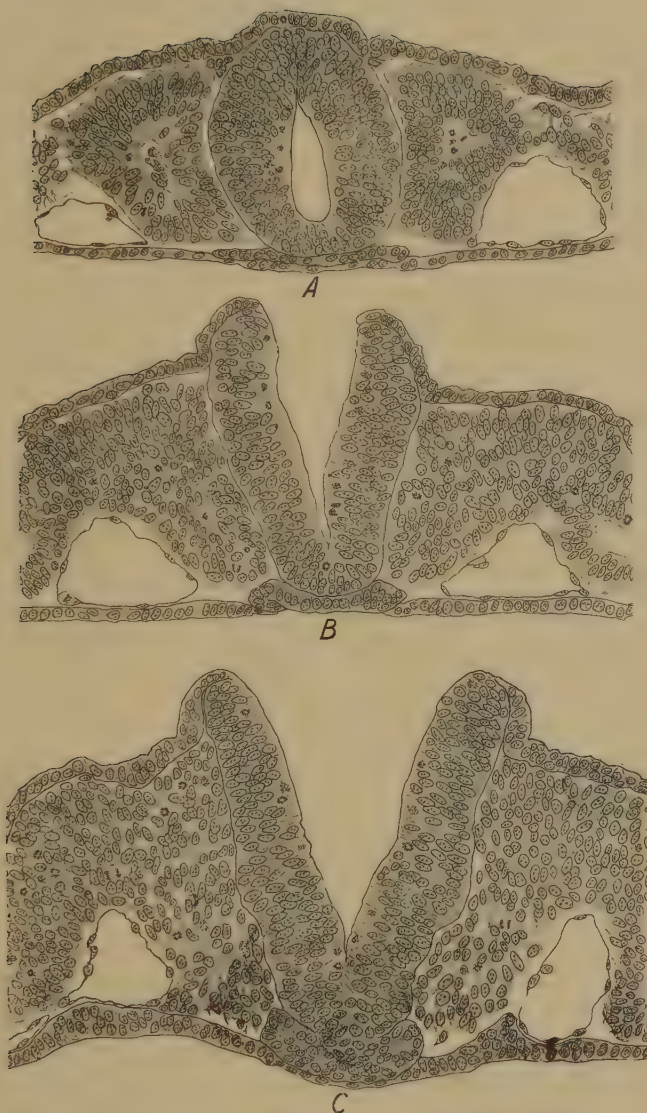


Fig. 13 A to C. Drawings of cross sections of an embryonic shield of the guinea pig removed 14 days and 11 hours after insemination. The entire series embraces 342 sections having $7\ \mu$ thickness. This embryonic shield possesses five pairs of somites with a sixth pair forming and presents early stages in separation of chordal plate from the entoderm. $\times 200$. A, 170th section, flattened chordal plate found between closed neural tube and entoderm; B, 252nd section, to the left border of chordal plate folded ventrally; C, 300th section, primitive streak region, chorda dorsalis in the act of separating from the primitive streak region.

structure presented in the drawing by the two opposed somites, the one cut through its middle, the other not. The chordal structure appears as a flattened plate, situated between the closed neural tube and the continuous entoderm. It would appear that in this region the borders of the split entoderm had grown toward the midline and fused. In B, of this series is reproduced a drawing of the 252nd section. This section approaches the region of the primitive node. There is present in this region an open neural groove. The chordal plate was fixed in the act of being rolled under, seen clearly only on the left side of the figure. These two figures, it would appear to me, evidence the two methods of separation of the chordal plate, from the entoderm—undergrowth of entoderm ventral to the chordal plate and infolding of the borders of the chordal plate. Especial attention has been given to the manner of the caudal extension of the chordal structures, caudal to the primitive node region, and, to the relative and absolute shortening of the primitive streak; by Lieberkühn in the guinea pig, Bonnet in the sheep and Keibel in the guinea pig and the pig. Exact measurements are presented which show that the primitive streak becomes relatively and absolutely shorter as development progresses. Though I present here no exact measurements, my own observations corroborate this, as may readily be ascertained on study of figures 4, 5, and 7, and on comparing these with figure 12, all of drawings of mid sagittal sections of progressive stages of development. The morphogenesis of the chorda dorsalis in the region caudal to the primitive node, namely in the primitive streak region, it would seem to me is well shown in C (fig. 13) the 300th section of this series. As is well known, in the axial portion of the primitive streak the ectoderm presents no basal limiting membrane. From the time of mesoderm anlage, ectoderm and mesoderm are in this region inseparably fused; the ectoderm here constituting the primary source of the mesoderm. With the stage when the chordal plate begins to separate from the entoderm, the ventral cells of the ectoderm-mesoderm mass in the primitive streak region begins to separate from the lateral mesoderm and from the overlying ectoderm proper, the latter differen-

tiating to form the neural plates, the sides of the neural groove and later neural canal, a definite basal limiting membrane separating the ectoderm of the neural plate and canal from the chordal structures developing. This it seems to me is in process of attainment in the region of the section sketched in C (fig. 13) the section passing through the caudal portion of the primitive node, no longer clearly defined. As may be observed on study of this section the chorda dorsalis is only in part differentiated, dorsally it is still in direct continuity with the floor of the neural groove. So far as my observations go, no definite chordal canal is to be observed in the primitive streak region and the term head process seems to be inappropriately applied to this structure in this region. From the region of the primitive node caudalward, the entoderm of the axial portion of this region at no time presents a ventral cleft, but at all stages in development passes as an uninterrupted layer, in close relation to the overlying mesoderm, but in no sense fused with it in the way that the ectoderm and mesoderm are fused in the primitive streak region. So far as I have been able to determine entoderm of this region takes no part in the morphogenesis of the chorda dorsalis and the latter can not be said at any time to be incorporated in the entoderm of this region. The two drawings reproduced in figure 14, are from a slightly older stage than that shown in figure 13. They are made from cross sections of an embryonic shield removed 14 days 12 hours after insemination. The series includes 300 sections of 10μ thickness. A (fig. 14) reproduces a drawing of the 132nd section. Ventral to the closed neural canal and between this and the continuous layer of entoderm, there may be observed a chordal plate in process of transformation to definite chorda dorsalis; the borders of the chordal plate appear in the act of turning in to form a chordal structure. B, of this series, reproduces a drawing of the 236th section, taken from the region of the anterior part of the primitive streak in which the chorda dorsalis is completely separated from both the ectoderm and entoderm, a completion of the process shown in its inception in C (fig. 13). The mode of the separation of the chorda dorsalis as here described is not quite the same as that given by

Keibel. From his studies on the embryonic shield of the pig, he is led to the following conclusion, given here in his own words:

Der Kopffortsatz muss auf Kosten des Primitivstreifens gewachsen sein. Dies Wachstum müssten wir uns so vorstellen, dass immer der vorderste Theile des Primitivstreifens sich in dem Kopffortsatz umbildet, und damit dem entsprechend das vordere Ende des Primitivstreifens zurückweicht.



Fig. 14 A and B. Drawings of cross sections of an embryonic shield of the guinea pig removed 14 days, 12 hours after insemination. The entire series embraces 300 sections of $10\ \mu$ thickness. Chordal plate nearly separated from entoderm, to form the chorda dorsalis. $\times 200$. A, 132nd section, arched chordal tube and closed entoderm; B, 236th section, chorda dorsalis separated from ectoderm of neural plates and the entoderm in the primitive streak region.

It has here been contended that the head process is a derivative of the primitive node and grows cephalad between ectoderm and entoderm and from its anlage is separated from the ectoderm by means of a distinct basal limiting membrane. Keibel's conclusion seems to me applicable only to that part of the chorda which develops caudal to the primitive node, in particular to the primitive streak region, the process resulting in an absolute shortening of the primitive streak and in the formation of a chorda dorsalis.

The development and relations of the anterior end of the chorda dorsalis have been the subject of special considerations in several investigations. In the guinea pig, as has previously been stated, the anterior end of the head process can be traced to the region of the future primary pharyngeal membrane. This is clearly shown in figure 5, and this question was discussed in connection with this figure. A definite chordal canal, so far as my material enables me to determine, does not develop to the anterior limits of the head process. The cells of the cephalic end of the head process, with nuclei arranged in one or two strata, come in very close relation with the underlying entoderm, so that at times it becomes difficult or quite impossible to differentiate clearly between cells of the head process and the underlying entoderm. I am led to conclude that the entoderm of this region at no time develops a distinct cleft, admitting of incorporation of head process in the entoderm. These observations are in the main in accord with those of Keibel, with reference to the cephalic end of the chorda anlage; his words read as follows:

Am schwierigsten liegen die Verhältnisse jedenfalls am Vorderen Ende des Embryos. Dort ist das Entoderm schon vor der Einschaltung der Chorda verdickt und, nachdem die Einschaltung geschehen ist, lässt sich beim besten Willen keine Grenze mehr zwischen den eingeschalteten Zellen und dem Entoblast erkennen.

Notwithstanding, Keibel is of the opinion, that the entire chorda dorsalis is developed from cell material derived from the head process. On further development, the cells of the head process, for a time intimately blended with the underlying ento-

derm, separate again from the entoderm; the two structures are then readily differentiated. Bonnet in his contributions to the embryology of the sheep contends that the anterior end of the chorda dorsalis is derived directly from the entoderm, the 'chordaentoblast.' This idea is developed and modified in his studies on the embryology of the dog. In this contribution he speaks of an 'Ergänzungsplatte des Urdarmstrangs' out of which develops the mesoderm of the anterior part of the head, the chorda of the anterior part of the head and a 'prämandibulares Darmrudiment.' In the guinea pig, as also previously determined by Keibel, such an 'Ergänzungsplatte' can not be differentiated, and I question its existence in other mammalia. In Grosser's preparation of a human embryo with chordal canal it was also impossible to determine definitely the anlage of the cranial end of the head process, his own words, omitting references to plates, read as follows:

"Ganz am cranialen Ende des Kopffortsatzes findet sich eine Region, in der die Abgabe von Material aus dem Entoderm an das Mesoderm nicht auszuschliessen ist (Protochordal—oder Ergänzungsplatte); doch ist die Konservierung gerade dieser Stelle wenigen günstig."

It has been the aim in this communication to present in successive stages, illustrated by figures drawn of sagittal and cross sections, the anlage and morphogenesis of the chorda dorsalis in the guinea pig, a form in which the successive stages of chordal development are relatively easily determined, by reason of size of structure and definition of stages, if suitable material is at hand. It is recognized that a comprehensive discussion of this fundamental problem, even so far as concerns only the amniotes, requires a comparison of results here obtained with observations made on other mammalian forms as also avian and reptilian forms. It is hoped that further study will admit of this. The observations pertaining to the guinea pig, as here briefly recorded, seem to me to warrant the following summary and conclusions:—

SUMMARY AND CONCLUSIONS

1. In the guinea pig, the head process has its anlage in the cranial border of the primitive node, an area of ectodermal proliferation, forming the cranial end of the primitive streak; by accretion of cells and proliferation of its own cells, the head process grows cephalad in the axial portion of the embryonic shield, primarily independent of the later wings of the mesoderm, to reach approximately the seat of the future primary pharyngeal membrane. At the caudal end of the head process, the cells of the head process are in direct continuation with the cells of the ectoderm of the primitive node region. Cranial to the primitive node the head process grows between ectoderm and entoderm, independent of each.

2. Soon after the anlage of the head process, its caudal end through rearrangement and growth of cells, acquires a lumen. The head process of this region differentiates to form the chordal canal. The chordal canal at no time in development extends to the cranial limit of the head process. The cranial end of the head process retains the character of a plate of cells, which fuse intimately with the underlying entoderm, so that its delimitation is for a time uncertain.

3. The chordal canal soon after its formation, through dehiscence of the ventral wall spreads out to form a chordal plate. With the dehiscence of the ventral wall of the chordal canal and the formation of a chordal plate, a cleft or split develops in the axial portion of the entoderm in the region of the chordal plate so that the lumen of the chordal canal becomes continuous with the cavity enclosed by the entoderm. This splitting of the ventral wall of the chordal canal and the underlying entoderm, in the guinea pig, takes place primarily in several regions, so that a series of discrete openings are formed, which fuse to form a longitudinally directed slit. The chordal plate is at no time definitely incorporated in the entoderm, the edges of the split entoderm, extending at all times to a greater or less degree under the borders of the chordal plate.

4. The chordal plate is then again separated from the entoderm to form the definitive chorda dorsalis, this either by a simple undergrowth of the edges of the cleft entoderm, the edges approximating and fusing, or by undergrowth of the entoderm accompanied by a ventral folding of the borders of the chordal plate. Both of the methods of separation of the chordal plate from the entoderm may be observed in different regions of the same embryonic shield.

5. In the primitive streak region the chorda dorsalis differentiates directly from the ventral part of the ectoderm-mesoderm mass of the axial part of the primitive streak, by separation from the lateral mesoderm and from the ventral part of the neural plates; this leads to a relative and absolute shortening of the primitive streak. In the region of the primitive streak, the entoderm, in all stages of development, retains its character as an uninterrupted layer.

6. An open neurenteric canal is not developed in the guinea pig; instead a neurenteric cord, not clearly defined, leading from the ectoderm to the entoderm, in the primitive node region.

7. This final conclusion seems warranted: Since the entoderm takes no active part in the histogenesis of the head process, chordal canal, and chordal plate and since the chordal plate becomes only partially and temporarily incorporated in the entoderm; there seems no justification for classing the chorda dorsalis as an entodermal derivative. And since the head process, the anlage of the chordal canal and derived structures, has its anlage in the cranial portion of the primitive node, a region of active ectodermal cell proliferation; and since the chordal canal and plate retain their continuity with the primitive node, which serves as a growth zone; there seems justification in regarding head process—chordal canal, and derived structures, chordal plate and chorda dorsalis—as a derivative of the ectoderm in the sense that the mesoderm is derived from the ectoderm of the primitive streak region of the embryonic shield.

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SOME CONSIDERATIONS REGARDING MICROSCOPICAL TECHNIQUE¹

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It has been said that the discovery of a new method may do more to advance science than the enunciation of a new principle. If this may, with any truth, be asserted of one method how really significant must be the comprehension of the technical aggregate upon which a science rests! Microscopical technique is variously regarded by biologists. To some it is an end in itself—a sufficient field for the exercise of all the powers of the investigator; to others it is a necessary evil to be endured only so far as it makes apparently satisfactory returns for the time spent. An exclusive acceptance of either position is a mistake leading to indifferent results. Technique is a tool, but an indispensable one, and, as yet, but imperfectly developed. It needs most careful study and merits all the care and attention we can devote to it. Progress in microscopic anatomy is largely dependent upon the refinement of present methods and the invention of new ones. Each serious student in this field of biology owes it to his chosen science to contribute something that is new or to suggest means for bettering the methods now in use. Rigid attention to all details of procedure is absolutely required in cytological investigations, and we may rightfully demand this of each worker as a prerequisite to the acceptance of his results. So much is the least we may ask—beyond this we can reasonably expect contributions to our present technical armamentarium. This expectation will be realized when the fundamental importance of the technical side of our work is appreciated and better means for its development are provided.

¹ An evening lecture delivered at the Marine Biological Laboratory, Woods Hole, July 27, 1917.

PROTOPLASMIC CONDITIONS

A consideration of the reaction between living protoplasm and chemical or physical agents must involve both members of the combination. Nothing is more obvious than the specificity of protoplasm, but changes which any particular variety may undergo are much less understood and appreciated. That there should be such a condition of variable reaction is no cause of surprise when the seasonal peculiarities of eggs under the same experimental conditions are recalled. Despite these facts there is little attention paid to the physiological condition of material submitted to the action of fixing fluids and stains, it being too generally assumed that the resulting differences in appearance are occasioned by the technique. Doubtless all experienced investigators can recall instances of inexplicable perversity on the part of apparently well understood materials and processes, resulting in such departures from the expected results as to raise grave doubts concerning the adequacy of our methods. Rarely, however, is the fault ascribed to the material and yet, as I hope to show, even the slightest modification of the protoplasmic element may markedly change the end result.

VALIDITY OF PHENOMENA

The importance of an exact knowledge of cell morphology increases from year to year as the conviction grows that in this structural unit are presented, in the most simple, available terms, the varied biological problems which engage our attention. In view of the fact that we rarely see a cell in its normal living condition the question becomes acutely serious regarding the adequacy of the phenomena we study in prepared material. This is a consideration to which thoughtful microscopists have given careful attention, and from many lines of evidence the conclusion has been reached that, in most respects, the product of our technique is representative of the living cell. It is hardly necessary to indicate the basis of this belief more than cursorily. Perhaps the most weighty evidence of this concordance is the high degree of uniformity in appearance obtained by the most

varied processes. Such variation as appears, in its major aspects, is clearly due to shrinkage, tearing, expansion or other physical changes which can reasonably be accounted for or predicted. Added to this is the close agreement in appearance between such details as are visible in the living cell and the same structures in fixed material. There is nowhere, in the variations under different systems of treatment, any suggestion of indefinite or unrestricted change, but only modifications of limited order involving a common series of elements everywhere recognizable.

SCOPE AND METHODS OF THE PROBLEM

While this uniformity exists, and is most encouraging, there is an accompanying variability in details which is often most annoying and puzzling. Where the purpose is to ascertain, down to the limit of vision, the exact architecture of the cell parts, this uncertainty of appearance may prevent the attainment of a confident judgment regarding some of the most significant cellular conditions. Since our effort should always be to reduce to their lowest limits the unknown variables in our problems the occurrence of these unpredictable changes in our materials is a constant challenge to the conscientious investigator.

So far our only method of attack has been largely through modifications of our empirical methods, but it has seemed possible to add to them some more reasonable means for determining the causes of our variables. Knowing the great interest all biologists must have in these fundamentals of our methods and realizing the insuperable difficulties in the way of the individual worker attacking alone the complexities of the problem, I am giving the results of a series of investigations upon microscopical technique, extending over a number of years, in the hope of contributing something to our common store of knowledge concerning the most trying, difficult and essential part of our work. In obtaining these results I have had the invaluable help of many of my students, among whom I am particularly indebted to Doctors Sutton, Carothers, Allen, Whiting and Hance. Without the thoughtful, efficient and discriminating help of Miss Ca-

rothers particularly it would have been impossible for me to have accomplished any large measure of the results so far obtained. Even with all this assistance my experience comprehends a relatively small range of materials and touches chiefly nuclear structures. Fortunately, from other sources, much information has been gained about cytosomic conditions, especially relating to mitochondria.

FRESHNESS OF MATERIAL

Some of the conditions involving protoplasm in its passage through technical treatment are fairly well understood and appreciated. The necessity for immediate fixation, for instance, appeals to most workers, but it is surprising to find the laxity which prevails even here. It is seriously advocated by some that a delay in fixation is desirable for the 'improvement' of the cell. Nothing is more certain however than that changes occurring after the death of the organism are, from the beginning, destructive. There is a possibility that some of these may favor the demonstration of certain structural details, but the inherent chance of error is so great that results obtained by this method could receive credence only when confirmed by more reasonable means. The extent to which post-mortem changes occur in a given period vary much with the nature of the material and the attendant physical conditions. In general there is a progressive liquefaction of the protoplasmic gels which eventually manifests itself in the prepared objects by vacuolization and loss of fine detail.

AGE OF SPECIMEN

In plant cells the changes incident to age are clearly marked and do not escape notice, but in animals these are less obvious and often fail to receive consideration. It is true that cleavage phenomena have been studied and the relation of nucleus to cytosome determined, together with the distribution of certain physiologically distinguishable substances, and Minot has given us a con-

ception of the nucleo-cytosome relation in adult cells, but we are yet lacking an understanding of the variations which must be ascribed to the age conditions of our prepared material. Without having made any careful study of this subject I have come to realize certain conditions in Orthopteran germ cells which must be due to the age of the organism. Among these are a greater density of the protoplasm, more of a tendency toward degeneration, and less precision in response to reagents. Hartman believes that there is an increase in size of the chromosomes with age. This is a subject which should receive careful attention.

METABOLIC CONDITION OF THE ORGANISM

At any given period in the life history of an organism the reaction of its cells to physical agents varies with metabolic conditions. This fact has been demonstrated in our experience with Orthopteran cells through changes resulting from the use of different food plants and through the invasion of the body by fungi. If *Chortophaga* is fed upon grass its reaction to fixation in Flemming, and to staining in haematoxylin, is such as to produce a pure nuclear stain after appropriate handling. Other animals of the same species, fed upon clover and subjected to the same technical treatment, show a reversed staining reaction. A similar reversal occurs in the cells of animals whose bodies are invaded by the mycelia of a fungus which not infrequently attacks grasshoppers. So profound is the change thus produced that it is practically impossible to secure a normal nuclear stain with haematoxylin.

METHOD OF KILLING

At first thought it would seem absurd to consider that the method of killing an animal would have any effect upon its cells, and yet it has been clearly proven that certain well marked differences obtain between the cytological details of animals killed by cyanide or by xylol. Ever since the beginning of my work

upon the Orthoptera I have been familiar with two contrasting conditions in the first spermatocyte metaphase. In one case the spindle is long and clean, the chromosomes extended and well distributed, and the cytoplasm clear and bright. Under the other condition the spindle is short and restricted, the chromosomes are contracted and crowded, and the cytoplasm is granular and hazy. Notwithstanding numerous efforts to produce these appearances at will by modifications of the different steps in the technical processes they remained unaccounted for. By exclusion and fortunate circumstance it was finally determined that killing the animal by dropping xylol upon it would eventuate in the extended spindle while animals killed by cyanide fumes would show cells with the contracted spindle. Experiments now under way have shown that like changes may follow other killing agents.

It has of course long been recognized that various animals require very careful treatment before they are subjected to the action of killing and fixing fluids. Unless they are narcotized they contract so strongly that their cells are useless for study. Some marine flat worms reduce themselves almost to the state of unorganized jelly under the action of ordinary fixing agents. That the relatively stable cells of the grasshopper could be influenced by the almost instantaneous process of killing did not occur to me, and in this respect I do not find myself alone, judging by the lack of published observations on this point. After the discovery of the actual facts and a careful consideration of the case the variations thus produced did not, after all, seem so strange. An animal, after death by cyanide, is limp and flaccid and there is no tendency for the jumping legs to break off. On the contrary, an animal killed by xylol is stiff and rigid and the jumping legs are either cast off or easily break from their attachment. If these lethal agents so differently affect the muscular and connective tissue cells it is not at all strange that other cellular complexes, including the germ cells, should manifest differential results. Whether the action upon the muscle fibers is the same as upon the spindle fibers is another matter,

but it would not be strange to find it so. Although experiments have not yet been carried far they indicate that the action of anaesthetics, like chloroform and ether, is similar to that of xylol, while decapitation produces the same result as cyanide. It is possible that the disturbances resulting from decapitation are due to alterations in the pressure of the body fluids but we do not have any definite information upon the final cause of any of these changes.

METHOD OF TREATMENT IN FIXING

While it is generally admitted that the tissue must be so exposed to the action of the fixative that ready penetration can be effected it is not so clearly appreciated that slight variations in the conditions existing at the time of fixation can produce extensive differences in the finished product. One of the most striking instances of this appears when the same form of material is treated with the same fixative, in one case being in a reasonable sized mass and in the other a smeared film. A fixative which gives atrocious results in the former case may produce good smear preparations. My experience has been that, with Orthopteran cells, almost any fixative will produce a good smear preparation. It must not be assumed that this is because no fixing agent is required, for this material, unlike the Hemipteran, cannot be fixed by drying but requires the immediate application of a fixative.

The size of the mass alone will not determine the character of fixation—immediate penetration and ready exchange of fluids must be provided for. In the study of *Culex* cells, as has been described by Whiting, Hance and Holt, although what appeared to be a good preservation was obtained by removing the abdomen and fixing the gonads *in situ*, when a careful study of the chromosomes was made this was found to be very poor. Indeed this method seemed to indicate that the diploid chromosome number is three, as has been asserted by two European observers, when, as a matter of fact, it is six. This is easily demonstrated by removing the gonad, freeing it of adherent fat and fixing in Flemming. Under these conditions the paired elements remain

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of the combination are important. It also appears evident that the presence of certain adjuvants contributes materially to the perfection of action in any given case. Thus the addition of urea to the picro-formal-acetic mixtures or to Flemming produces well marked and characteristic effects upon both plant and animal cells. Various sugars and malic acid correspondingly improve the action of fixatives upon plant cells, each producing a distinctive reaction. In general the action of these inert substances is to preserve the more fluid parts of the nucleus, so that otherwise empty spaces are shown in sections to be filled with a delicate reticulum. Increased concentration or specific action may however result in vacuolization of the cytoplasm. The great advantage of these additions to the fixing fluid for chromosome studies is in preventing the somewhat liquid chromatin of certain cells from flowing together with the consequent loss of chromosome outlines.

PHYSICAL CONDITIONS DURING FIXATION

Little attention, relatively, has been paid to the physical conditions under which the protoplasm and its coagulant are brought together, and yet this is far from being an unimportant matter. Temperature, concentration of the reagents, method of application, the presence of adjuvants and many other circumstances are significant. I wish here to speak particularly of the relation of temperature to the fixation process. The optimum conditions appear to vary both with the material and with the fixative. It seems generally true that for mammal tissues a temperature of 0°C. with Flemming, and 38°C. with picro-formal-acetic is best. There seems to be less difference in the case of invertebrates but this is dependent somewhat upon the rapidity of penetration. Our experience so far would seem to indicate that if immediate action is secured, as in a film, the temperature is not important, but that if time is required to bring the cell and reagent together it should be considered. The explanation for the variation in temperature required to produce equally good results would seem to be that a low temperature holds the tissue

unchanged during the period required for the penetration of a slowly moving reagent, while the higher temperature raises the rate of penetration of the fixative which is thus brought to the cell before it can undergo alteration. Of course with so high a temperature as 100°C. the action is directly that of the heat.

WASHING

Once the protoplasm is coagulated by fixation we are then dealing with a solid instead of with a semi-fluid substance, but this does not signify that the object can be treated with any less care. In fact many of the poor preparations which we see are the result of neglect in after-fixation stages. Without exaggeration it can be said that the best of fixed material may be spoiled at almost any period of its subsequent treatment. I should like to give some examples of these changes which have appeared during the course of our experiments, beginning with the next step of washing out the unused fixative from the cell. According to all directions this should be thorough, but apparently the principal object sought is to remove an extraneous substance for physical reasons. It seems certain, however, that marked differences in a fundamental staining reaction may follow in tissues which would commonly be regarded as well washed, due to the further extraction of chemical substances. Haematoxylin, while not a test for chromatin, nevertheless, under ordinary conditions, gives a pure nuclear stain with sufficient extraction. This was the universal result in all my own Flemming preparations, but every year when students in my cytology class made slides from fresh material they secured a reversed staining reaction, the nucleus being unstained and the cytoplasmic structures darkly tinged. Finally the yellow color of the nucleus in these latter cases, together with the amount of color in the alcohol which had stood for some months on my own unsectioned material, suggested that possibly insufficient washing was responsible for the reversal of stain. To test this out paraffin sections were made of recently fixed material, which had been washed as usual for twenty-four hours, and the ribbon

spread and dried. The paraffin was removed with xylol from the sections at one end of the slide and left protecting the other half. Thus prepared the slide was soaked in seventy per cent alcohol for three days, after which the paraffin was dissolved from the remaining sections and the whole slide stained in iron-haematoxylin. Upon differentiation a very peculiar slide resulted, one end showing cells with a pure nuclear stain, the other exhibiting excellent mitochondria but no stained chromatin. The length of washing is thus shown to be the means of securing a mitochondrial stain or a chromatic stain with the same material and the same reagents. With other fixatives no such results might follow and, in some, washing can be omitted completely. This part of the procedure must be dictated by the character of the material, the nature of the fixative and the object sought.

DEHYDRATING

In dehydrating extensive shrinkage, distortion and tearing may result. The gross differences thus produced have been considered by Allen in a recent paper, where it is stated that the major portion of shrinkage in the whole series of technical processes comes during dehydration. Besides these more general effects upon the whole tissue there are possible local changes within the cell which are significant. There has been extended discussion of the phenomenon of synzesis, much of it being fruitless and uncalled for. In an early paper I stated that this condition in the Orthoptera is an artifact and suggested that possibly it might be of similar character in other cases. This incidental remark has been more quoted and discussed than many of my most important statements. In this case synzesis is purely an artifact resulting from the too sudden passage of the material from one fluid to another. It never occurs in properly dehydrated material and, while it may not always result from sudden dehydration there is the possibility of it, which should be avoided by gradual removal of water. Aside from this question of synzesis, which probably is not nearly so important as it has seemed to some, there are many other changes produced by alcohol which need not be discussed here.

CLEARING

Removal of alcohol by some agent miscible with it, on one hand, and with paraffin on the other, may be attended with some of the same difficulties connected with dehydration, which can be avoided in large part by the proper selection of the agent and by its careful application. Shrinkage and hardening are the worst evils which follow the use of clearing agents. Some years ago I tested the shrinkage action of various substances upon young chick embryos and found that while some of them reduced the dimensions of the disc almost a half, others caused a contraction of less than ten per cent. The least injurious of these was cinnamic aldehyde following eighty-five per cent alcohol. Allen reports that aniline oil, after seventy-five per cent alcohol, produces no appreciable diminution in volume even after twenty-four hours' action. While we have no exact data on the subject it seems certain that the gradual transition from alcohol to the clearing fluid results in distinct advantages.

INFILTRATION

One of the worst difficulties in the paraffin method is the shrinkage and distortion which comes from the application of the hot paraffin. So severe is this action that the method is entirely inapplicable after certain fixatives. I have already referred to the fact that good smears may be secured by almost any fixation, but material fixed in Vej dovský's chrome-sublimate or with Helly's modification of Zenker suffers such contraction in the hot paraffin as to be useless for study. That this shrinkage and distortion occurs during infiltration was demonstrated to me by Doctor Danchakoff who carried some of the same Zenker-formal material through the celloidin process with excellent results. Doubtless much condemnation of fixing methods is unjust because the other circumstances attending the technique have not been properly appraised. There are some tissues also which can not be carried through the paraffin method because they are either too hard or too soft to withstand its action.

SECTIONING

During the process of sectioning changes of great moment may occur, many of which are familiar to all experienced workers. I need not speak of such effects as compression, tearing, splitting, folding and cracking of paraffin sections because they are obvious to all. Less marked, but of great importance in chromosome studies, is the removal entire of chromosomes which are either lost or carried over into neighboring cells to cause double confusion. Extreme care is needed in sectioning—the knife must be perfectly sharp, it must be inclined to the plane of the section at exactly the right angle, the paraffin should be homogeneous and of a density suited to the material, and the room temperature must be adapted to the thickness of the sections required. The resulting ribbon should consist of sections little less in diameter than the face of the block from which they were cut—straight, free from scratches or breaks and of uniform thickness. Such can be obtained only by the most exacting care in detail but are essential to good results.

SMEARING

If the smear method is employed it should be carefully checked by a study of sections. Properly used it is a valuable method but there are many difficulties attending it. Some material, like blood or the germ cells of the Hemiptera, may be distributed over a glass surface and fixed by drying, but the same procedure applied to Orthopteran cells results in a featureless expanse of unorganized material. Such cells must be distributed between two covers with exactly the right pressure, the covers separated just so and the films fixed at once. The covers should be of the correct diameter for the amount of material between them and the pressure applied adapted to the density of the cells of that particular species. With the utmost care the cell elements suffer various distortions which must be recognized by comparison with sections. Some cells can not be smeared at all because of their fluid character and it is not uncommon in the best smears to find apparent multinucleate cells resulting from the fusion of sepa-

rate cells before fixation. It is almost literally a fact that one may find nearly any condition imaginable in a smear. The need for great caution is therefore clearly manifest.

STAINING

Time will not suffice for any adequate consideration of the process of staining. The number of conditions to be demonstrated, the variety of the staining agents available and the complexities of the processes are too great for anything less than a monographic treatment. I wish merely to call attention to the adequacy of two or three well understood stains for all general purposes. Iron-haematoxylin alone will serve to demonstrate almost all nuclear and cytoplasmic structures which can be specifically distinguished by other agents. If to the use of this is added the safranin—gentian violet—orange G. combination the cytologist is prepared for almost any condition aside from the most special studies.

MOUNTING

It would seem to be the opinion of some cytologists, judging by their preparations, that once the sections are obtained any method of getting them on the glass will do. And yet, just at this point the greatest care is needed if any size comparisons are to be made. A complete and uniform spreading of the ribbon is absolutely required and no pains should be spared to secure it. I do not hesitate to say that unless this step is properly taken conclusions regarding size and form of cell structures are almost worthless. A matter of apparent small importance is the straightness of the ribbons on the slide, but this mole hill may well become a mountain of difficulty in an extended study and materially reduce the effectiveness of the observer. A little time expended during the preparation of the slide will save much, later, and may even be the determining factor between good and bad results.

CRITERIA OF JUDGMENT

It may seem somewhat aside from a discussion of technical problems to consider the subject of criteria of judgment in micro-

scopic anatomy, and yet it is so intimately a part of the whole problem of interpretation involved that I can not refrain from speaking of this most essential and neglected phase of the work. Under the microscope things are not what they seem—every image produced by the lenses must be interpreted in the light of the observer's experience. The microscopical appearance of a sphere of air in water is about as widely removed from that of the actual object as could well be imagined. Many cellular structures require the same translation by experience when studied microscopically. The literature of chromosome studies alone is filled with false interpretations and worthless theories because of the neglect of this elementary conception of microscopical images. In most instances we study colored images, but these are superimposed upon refraction images and the distinction is not always realized, with the result that there are descriptions of longitudinally split rods in which the split is really a refraction line or of divided threads which are only hollow tubes. Even more obvious errors than these are frequently made. A glance at the figures of metaphase chromosomes in many papers will show them to vary in diameter strongly and to have pointed ends. Neither of these conditions normally obtains and their representation is due to the fact that the observer neglected to note that these apparent variations are due to a failure to focus each region at its optical section. Thus the fundamental organization of the chromosome is misrepresented because the observer has not realized that a knowledge of the third dimension of his object must be gained by focusing the microscope. If such an elementary knowledge of microscopical conditions appears lacking in an observer's work the experienced investigator at once suspects graver defects and discounts both the observations and the conclusions. No one can afford to place himself in an unfavorable light at the very beginning of his presentation by the neglect of the fundamentals of the science.

CONDITIONS OF MICROSCOPICAL OBSERVATION

There are many considerations involving the choice and use of the microscope and its accessories, the manipulation of the

light and the substage condenser, the comparison of images produced by high and low magnification, etc., which are of the utmost importance in exact microscopical observation, but which I have no time to discuss here. I can not refrain from saying, however, that every microscopist should understand thoroughly the instrument upon which he depends. Without such an understanding his results are sure to lack precision and accuracy.

THE PERSONAL FACTOR

There is one matter upon which I should like to speak, but hesitate to do so for fear of being misunderstood. Since it is one of such fundamental importance however I shall venture to express myself freely, trusting to the good judgment of my readers to take what I say in the spirit of helpfulness in which it is intended. An experience, which I am surprised to find extending to twenty years, has taught me that cytologists, like poets and other specialized individuals, are born to their work and can with difficulty, or not at all, be diverted into it. There are certain qualities, the possession of which is no warrant for undue self esteem, that are demanded of the person who would devote himself to the investigation of the intricacies of cellular phenomena. Without these, disappointment is bound to come to the individual and trouble to his fellow workers. The literature is burdened with papers which were at best doomed to a fruitless existence because their authors were not qualified by nature or training for the work which they undertook. In full recognition that this same statement may with truth be made of many other lines of endeavor, I would still say that it is particularly true of the exacting work of cytological observations. It does not follow even that because a man is a good histologist or embryologist that he will make a successful cytologist. There is no other type of work with which I am familiar that calls into play so strongly the qualities of infinite patience and care, the nicety of manipulation, the exactness of observation, the discrimination of values, the judgment of relations, the exercise of good common sense together with the need of well balanced con-

structive imagination, as does the finest cytological work. Before any person should decide upon the career of a cytological investigator he ought to demonstrate to some experienced worker the possession of the necessary qualifications for it. Even then, only time and a long suffering scientific public will be able to tell whether in his case the eminent cytologist was as good a judge of men as of cells.

FURTHER OBSERVATIONS ON THE RELATIVE SIZE AND FORM OF THE RIGHT AND LEFT TESTES OF PIGEONS IN HEALTH AND DISEASE AND AS IN- FLUENCED BY HYBRIDITY

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In an earlier paper in this Journal the writer¹ published data for the weights of the right and left testes of nearly 200 doves and pigeons, and measurements of the length and breadth of 78 pairs of these. In the present paper the weights for 300 additional pairs of testes are given and measurements are supplied for more than 500 additional pairs.² The earlier results based on relatively small numbers indicated (1) that among pigeons the right testis is larger than the left in a very high proportion of cases; (2) that the left testis, though smaller in size, is nevertheless usually longer (and narrower) than the right; (3) that the testes suffer very pronounced atrophy in disease—particularly in tuberculosis; and (4) that the normal size relation of the two testes is probably more often reversed in hybrids; and further that the “number of these reversals seems to increase with the degree of hybridization, that is, with the width of the cross.” The results given in the present paper leave little or no doubt on any of these topics; an adequate demonstration of these four points, however, requires the detailed presentation of the new data.

The results now at hand, moreover, warrant a consideration not hitherto attempted of the changed or reversed normal size relation of the two testes of hybrids. The fact, and the significance of the fact, of the frequent reversal of the size and form of the

¹ Riddle, O. Size and length relations of the right and left testes of pigeons in health and disease. *Anat. Rec.*, vol. 11, October, 1916.

² A classified summary of the weights of still another 102 pairs of testes is given (table 28) at the end of this paper.

testes of hybrids from widely separated forms (genera)—as this may now be seen in the light of the control of sex obtained by Whitman³ and later by Riddle⁴—is the chief new point for present consideration in this paper. But the data concerned with the several questions connected with the size and length relations of the two testes should be examined first.

We may here restate some of the reasons for interest in data on the size and form relations of the right and left testes of birds. In the earlier report the following statement was made:

The right ovary undergoes an early and more or less complete atrophy in most species of birds. Erzold ('91) has shown that in the sparrow the left testis is larger than the right. Firket ('14 and Swift ('15) have shown that in the chick embryo there were more primordial germ cells in the left gonad, and that this gonad is there also distinctly larger than the right. Allen ('07) found that the sex cells were unequally distributed to the two gonads of the turtle (*Chrysemys*), the left receiving most. In this form only 24 to 70 per cent of the sex cells ever enter the gonads. Our own accumulation of data on the size and length relations of the two testes of young and adult pigeons show a very decided predominate number of larger right testes; and also a distinct difference in shape of the two glands—the left though actually smaller in size is usually absolutely longer than the right.⁵ Changes in the size relation in birds dead of certain diseases—particularly tuberculosis—and in hybrids, are also suggested by our data.

The meaning of this pronounced inequality in the distribution of the primordial germ cells which is plainly associated with a larger left embryonic gonad, and the finding in adults of two groups of birds of a nearly constantly larger gonad, but this a different gonad in the two cases, is by no means clear. But, whatever this may mean, it is probably a situation of importance to the theory of sex.

An examination of our data has shown that the measurements of glands of healthy birds should be grouped apart from those dead of disease; and those of pure species should be separated from hybrids. The justification of these separate groupings will appear later (pp. 87–88).

The testes of pigeons suffer great reduction of size in disease—particularly tuberculosis. It is probable that the right gland suffers

³ Posthumous Works, vol. 2, The Carnegie Institution of Washington (in press).

⁴ See Riddle, O. The control of the sex ratio. *Proc. of the Wash. Acad. of Sci.*, vol. 7, no. 11, June, 1917; and several earlier papers.

⁵ Present data show that this statement should be "longer than the adult right." The very young were not separately classified or studied in the earlier paper, and measurements were reported for only a very few such individuals.

TABLE 1
Summary of previous data

CLASS	STATE	WEIGHT RELATIONS			LENGTH RELATIONS		
		L +	L =	L -	L +	L =	L -
Pure species.....	Healthy	0	0	5	0	0	3
	Diseased	9 ²	6 ²	31	14	2	2
Common pigeons.....	Healthy	5	0	27	1	0	0
	Diseased	2	0	8	2	2	1
Specific hybrids.....	Healthy	6	7	19	8	6	7
	Diseased	10	11	24	15	1	4
Generic hybrids.....	Diseased	7	0	12	2	1	6
Total healthy		11	7	51	9	6	10
Total diseased		28	17	74	33	6	14
Grand total		39	24	126	42	12	24

¹ The cases of larger left testis are grouped under L +; those of equal size under L =; those with a smaller left testis under L -.

² Five of the (9), and 3 of the (6), are from 14 *Sp. surattensis* (earlier mis-called *Sp. tigrina*)—all dead at less than 9 months old.

greater reduction than the left. The left (persistent) gonad of the female does not undergo a similar reduction in tuberculosis (p. 102).

The very considerable significance of the reversal in hybrid pigeons of the normal size relations of the two testes will be treated later.

A summary of the data available for the earlier publication is reproduced here in table 1. The 'length relations' of the two testes are shown in the last three columns of the table. The results are as stated above. The details of these data were thought to indicate that the smaller left testis is longer and thinner than the right. In this connection it was observed (p. 99) that:

This difference in form is perhaps not without interest since the only persistent gonad in the female—that of the left side—is characteristically 'thin' and 'long.' The testis that develops on this side is similarly characterized as compared with its mate of the right side.

In order to obtain a quantitative expression of the form differences of the gonads in young birds of the two sexes table 2 has been prepared. For this purpose healthy males and females of similar age were killed. Young birds (3 to 7 weeks) were chosen instead of mature ones because the functional ovary becomes much enlarged and distorted by the ripening of the follicles; and further, because such an investigation was not included in our earlier report. The figures for the females show the almost, or quite, complete atrophy of the right ovary in most of these young doves. Four of the 21 retained right ovaries of measurable length. Two other points of interest attach to these data. First, the single, persistent (left) ovary is fully twice as long as is either of the double organs (testes) present in the male. Second, in these very young males the two testes are not of markedly different length; but the slight difference that exists, at this stage, indicates a shorter left testis—not the longer one which is normal for healthy adult birds of pure species. Observations on the testes of many hundreds of males at still younger stages than that represented by the birds of this chart has fully convinced the writer that in the just-hatched squab the right testis is normally longer and larger than the left. We do not know whether the right testis is proportionately longer at this time. Females at the hatching stage normally show, on the other hand, decidedly longer and larger left ovaries. It is not easy to measure breadth and thickness of these ovaries. All who have seen the ovary of the young dove know that it is a quite thin tongue-like organ with a broader anterior and a more tapering posterior extremity, and with a somewhat roughened or irregular outline.

SIZE AND FORM OF TESTES OF HEALTHY ADULT DOVES OF PURE SPECIES

Weights and measurements for the testes of 24 doves are given in table 3. In only 2 of the 24 is the left testis the larger, and in both of these cases the size difference is slight (0.7 per cent and 4.5 per cent). The length relations of the right and left testes of this group is, however, quite different. Although 22 of the

TABLE 2
Comparison of testes length, with ovarian length in healthy young doves (killed April 20, 1917)

CLASS	MALES			FEMALES			
	No.	Length and width in millimeters	Per cent of difference	No.	Length (mm.)	No.	Length (mm.)
Pure species.....	E515	R = 5.5 x 1.1 L = 5.5 x 1.3	= 0.0	E532	R = 0.0 L = 10.5	E408	R = trace L = 12.5
	K416	R = 5.5 x 0.5 L = 4.0 x 0.5	- 37.5	K387	R = 0.0 L = 10.5	K360	R = 11.0 L = 11.5
	E418	R = 5.8 x 1.6 L = 6.3 x 1.5	+ 8.6	B463	R = 0.0 L = 12.0	E408	R = trace L = 12.5
Specific hybrids.....	E667	R = 5.6 x 1.0 L = 5.4 x 1.0	- 3.7	K358	R = trace L = 12.2	K454	R = 0.0 L = 10.5
	E574	R = 6.1 x 1.6 L = 5.5 x 1.5	- 10.9	K308	R = 0.0 L = 9.0	K386	R = trace L = 9.0
	K364	R = 5.0 x 0.8 L = 4.9 0.7	- 2.0	K375	R = 4.0 L = 9.0	K380	R = 11.0 L = 11.5
Tri-specific hybrids.....	K406	R = 5.2 x 1.0 L = 4.3 x 1.0	- 20.9	K317	R = trace L = 17.0	K341	R = trace L = 13.0
	K443	R = 5.0 x 0.9 L = 3.8 x 0.9	- 31.6	K354	R = 0.0 L = 11.0	K420	R = trace L = 12.0
	K427	R = 4.3 0.9 L = 5.3 x 0.9	+ 23.3	K345	R = 4.8 L = 15.0	K373	R = 2.8 L = 11.0
Generic hybrids.....	K383	R = 6.9 x 1.3 L = 6.7 x 1.0	- 2.9	K398	R = 0.0 L = 11.0		
	K307	R = 4.8 x 1.0 L = 4.8 x 1.0	= 0.0	K407	R = trace L = 14.0	K303	R = 0.0 L = 11.0
Average length.....	(11) ♂	R = 5.4 L = 5.1	Average	(11) ♀	R = --? L = 11.6	(10) ♀	R = --? L = 10.5

TABLE 3
Weights and measurements of testes of healthy adult doves of pure species—killed April 12, 1917

NO.	WEIGHT	PER CENT OF DIFFERENCE	LENGTH AND WIDTH	PER CENT OF DIFFERENCE	NO.	WEIGHT	PER CENT OF DIFFERENCE	LENGTH AND WIDTH	PER CENT OF DIFFERENCE
E90	R = 0.514 L = 0.396	- 29.8	17.3 x 7.3 16.8 x 6.8	- 2.9	E2	R = 0.640 L = 0.572	- 11.9	21.8 x 7.1 24.2 x 6.5	+ 11.0
E464	R = 0.544 L = 0.430	- 26.5	19.2 x 6.9 23.4 x 5.2	+ 21.8	E338	R = 0.765 L = 0.616	- 24.2	20.3 x 8.3 20.6 x 7.0	+ 1.4
E151	R = 0.752 L = 0.685	- 9.8	21.1 x 8.3 23.1 x 6.5	+ 9.5	A713	R = 0.854 L = 0.676	- 26.3	25.0 x 8.5 21.4 x 7.7	- 16.8
E468	R = 0.186 L = 0.129	- 44.2	12.2 x 5.5 11.5 x 3.7	- 6.1	E559	R = 0.512 L = 0.535	+ 4.5	18.8 x 7.5 21.9 x 6.6	+ 16.5
E592	R = 0.145 L = 0.137	- 5.8	12.2 x 4.9 13.2 x 4.0	+ 8.2	E480	R = 0.669 L = 0.423	- 58.1	20.8 x 7.8 19.4 x 6.3	- 7.2
E410	R = 0.961 L = 0.745	- 28.9	22.8 x 8.7 22.2 x 7.3	- 2.7	A666	R = 0.774 L = 0.642	- 20.5	22.4 x 8.4 24.2 x 6.7	+ 8.0
E448	R = 0.726 L = 0.564	- 28.7	18.5 x 8.4 18.6 x 7.2	+ 0.5	B318	R = 0.705 L = 0.702	- 0.4	20.0 x 8.2 22.1 x 7.5	+ 10.5
E263	R = 0.388 L = 0.259	- 49.8	17.3 x 6.4 17.1 x 5.0	- 1.1	E389	R = 0.570 L = 0.500	- 14.0	19.3 x 7.3 22.4 x 6.8	+ 16.1
E355	R = 0.683 L = 0.568	- 21.1 ¹	19.5 x 8.2 23.4 x 6.6	+ 20.0	B289	R = 0.412 L = 0.261	- 57.8	15.2 x 6.9 15.8 x 5.3	+ 3.9

E486	{ R = 0.575 L = 0.579	+ 0.7	17.4 x 8.3 21.2 x 7.0	+ 21.8	{ P5 ²	{ R = 0.139 L = 0.105	- 32.4	10.7 x 4.7 9.6 x 4.2	- 11.4
E330	{ R = 0.598 L = 0.573	- 4.3	18.5 x 7.9 20.0 x 7.5	+ 8.1	{ A615	{ R = 0.854 L = 0.679	- 25.7	22.3 x 8.5 23.1 x 7.7	+ 3.6
E117	{ R = 0.931 L = 0.743	- 25.3	22.8 8.7 23.8 x 7.4	+ 4.4	{ E236	{ R = 0.673 L = 0.595	- 13.1	17.2 x 8.2 20.3 x 6.7	+ 18.0

¹ From this point doves were killed April 18, 1917.

² Tuberculosis found in joints of wing and legs.

24 left testes are smaller than their associated testis, 17 of them have a greater length than their larger associates. A comparison of the figures for "per cent of difference" for size and for length shows, moreover, that in all cases, without exception, the left testis is relatively more elongate than the right.

SIZE AND FORM OF TESTES OF DISEASED ADULT DOVES OF PURE SPECIES

The 20 diseased adult doves of table 4 show 3 smaller right testes and 4 additional pairs in which the two testes were of equal size.⁶ The enormous reduction in size of the testes of diseased birds is made clear by a comparison of the figures given in tables 3 and 4. In health the right testis of most, probably all, of these birds weighed between 0.500-1.000 g. Weights of 0.016 or 0.025 g. in adult birds (e.g., 924, A335) dead of disease, but known earlier to have been fully functional and fertile, indicate that fully 95 per cent of the weight of the gland was lost under disease. An inspection of the figures in this table, and in the succeeding tables in which the cause of death is recorded, will make clear a further point, namely, that tuberculosis is the disease associated with the most extreme atrophy of the testes. It was noted in our earlier paper that probably no reduction whatever occurs in the ovary of tubercular females. A suppression of ovulation and a cessation of the growth and development of follicles⁷ plainly occur in the ovary of the female, but the total size of the gland proper is not reduced.

⁶ The number of pairs of testes recorded as of 'equal size' is necessarily larger in those series (diseased and young) in which very small glands predominate. Weighings were usually made to milligrams only, and differences in the two gonads were recorded only in cases where the difference was beyond question.

⁷ The largest follicles that can be found in the ovaries of doves (of most species) dead of very advanced tuberculosis are rarely more than 1.5 mm. in diameter; the number of smaller but plainly visible follicles in such ovaries is, however, usually quite large.

TABLE 4

Weights and measurements of adult doves of pure species¹ dead of disease²

NO.	DATE	DISEASE	WEIGHT	PER CENT OF DIFFERENCE	LENGTH AND WIDTH	PER CENT OF DIFFERENCE
A111	July 23	(Cause ?)	$\left\{ \begin{array}{l} R = 0.052 \\ L = 0.031 \end{array} \right.$	-67.7	$\begin{array}{l} 10.7 \times 3.3 \\ 10.7 \times 2.7 \end{array}$	= 0.0
578	August 13	(Cause ?)	$\left\{ \begin{array}{l} R = 0.040 \\ L = 0.025 \end{array} \right.$	-60.0	$\begin{array}{l} 9.1 \\ 8.6 \end{array}$	- 5.8
123	October 8	Sp., li., lu.	$\left\{ \begin{array}{l} R = 0.035 \\ L = 0.036 \end{array} \right.$	+ 2.8	$\begin{array}{l} 7.4 \times 3.0 \\ 8.4 \times 3.0 \end{array}$	+13.5
A165	October 10	Sp., li.	$\left\{ \begin{array}{l} R = 0.041 \\ L = 0.026 \end{array} \right.$	-57.7	$\begin{array}{l} 8.4 \times 2.6 \\ 7.8 \times 2.2 \end{array}$	- 7.7
A350	October 22	Li., sp.	$\left\{ \begin{array}{l} R = 0.515 \\ L = 0.344 \end{array} \right.$	-49.7	$\begin{array}{l} 20.9 \times 6.7 \\ 20.3 \times 6.5 \end{array}$	- 2.9
E416	November 7	Lu., sp.	$\left\{ \begin{array}{l} R = 0.032 \\ L = 0.032 \end{array} \right.$	= 0.0	$\begin{array}{l} 6.7 \times 2.5 \\ 6.6 \times 2.6 \end{array}$	- 1.5
B688	December 6	Intest.	$\left\{ \begin{array}{l} R = 0.072 \\ L = 0.075 \end{array} \right.$	+ 4.1	$\begin{array}{l} 9.6 \times 3.5 \\ 8.8 \times 5.2 \end{array}$	-9.1
494	December 16	Li. (fighting)	$\left\{ \begin{array}{l} R = 0.164 \\ L = 0.148 \end{array} \right.$	-10.8	$\begin{array}{l} 11.0 \times 5.8 \\ 13.3 \times 4.4 \end{array}$	+20.9
A335	December 29	Lu., li., sp.	$\left\{ \begin{array}{l} R = 0.025 \\ L = 0.021 \end{array} \right.$	-19.0	$\begin{array}{l} 8.7 \times 2.4 \\ 8.6 \times 2.0 \end{array}$	- 1.2
990	January 8, 1917	Sp., li.	$\left\{ \begin{array}{l} R = 0.033 \\ L = 0.029 \end{array} \right.$	-13.8	$\begin{array}{l} 8.7 \times 2.5 \\ 8.5 \times 2.5 \end{array}$	- 2.3
A345	January 21	(Cause ?)(juv. ?)	$\left\{ \begin{array}{l} R = 0.012 \\ L = 0.012 \end{array} \right.$	= 0.0	$\begin{array}{l} 6.6 \times 1.7 \\ 6.0 \times 1.9 \end{array}$	-10.0
E204	January 27	(Ascaris)	$\left\{ \begin{array}{l} R = 0.071 \\ L = 0.095 \end{array} \right.$	+33.8	$\begin{array}{l} 7.2 \times 4.2 \\ 10.5 \times 3.8 \end{array}$	+45.8
182	January 30	Sp., li., hem.	$\left\{ \begin{array}{l} R = 0.500 \\ L = 0.455 \end{array} \right.$	- 9.9	$\begin{array}{l} 18.7 \times 8.3 \\ 22.0 \times 6.4 \end{array}$	+17.6

TABLE 4—Continued

NO.	DATE	DISEASE	WEIGHT	PER CENT OF DIFFERENCE	LENGTH AND WIDTH	PER CENT OF DIFFERENCE
924	February 22	Li., sp.	{ R = 0.016 L = 0.016	= 0.0	6.8 x 2.1 8.0 x 1.9	+17.6
A41	March 20	Li. and sp.	{ R = 0.125 L = 0.100	-25.0	11.7 x 4.2 12.2 x 3.7	+ 4.3
994	March 23	Sp., liver	{ R = 0.028 L = 0.027	- 3.7	8.0 x 2.1 — x 2.0	?
A332	March 31	Li., sp.	{ R = 0.019 L = 0.017	-11.8	6.8 x 2.0 7.7 x 1.4	+10.3
B601	April 3	Intestine (?)	{ R = 0.480 L = 0.391	-22.8	22.2 x 7.0 22.4 x 6.0	+ 0.9
A861	April 7	Weakling	{ R = 0.055 L = 0.048	-14.6	9.5 x 2.7 9.9 x 2.5	+ 4.2
Gs	April 16	Sp., li.	{ R = 0.007 L = 0.007	=0.0	3.8 4.5	+22.2

¹ Some young offspring of blond ring dove 'mutations' (?) are included in this list.

² Abbreviations of the names of organs to their first two letters, implies that advanced and very evident tuberculosis was found in those organs (lungs, spleen, liver, joints, mesentery, intestine). When more than one organ was affected the name of the organ (or organs) apparently most affected is written first. When the word is written out it denotes that this organ was abnormal, but not necessarily tubercular. Immature birds are designated (juv.). References to hemorrhage (hem.) and abdominal wall (abd.) are also given as here indicated.

SIZE AND FORM OF TESTES OF HEALTHY YOUNG DOVES OF PURE SPECIES

In table 5 are given the measurements of 29 pairs of testes of healthy young doves of pure species (2 in table 2), and the weights of 4 of these pairs. These few pairs of testes show no reversals of size from the order usual for the adults. The measurements indicate that in 17 of the 29 pairs the left testis was the longer, in 3 pairs they were of equal length, and in 9 pairs the right was the longer. It should be noted that the birds of this series, and of succeeding tables of 'young doves,' were of somewhat more advanced age (5 to 12 weeks) than were those taken for the special purposes of table 2.

SIZE AND FORM OF TESTES OF HEALTHY ADULT COMMON PIGEONS

In tables 6, 7 and 8 are given the weights of 49 pairs of testes of healthy adult common pigeons. In 12 of these pairs the left testis was larger than the right, in 36 pairs smaller, and in one case the two glands were of equal size. These figures indicate a higher proportion of 'reversals' of the normal size relations than was found in Columbidae of pure species; and there are good reasons for believing that more than one wild species has entered into the stock which has given rise to the several scores of races of domestic or fancy pigeons.

Measurements for 53 pairs of testes are given in these same tables. The left testis is the longer in 25 pairs, shorter in 27 pairs, and of equal length in one pair. Since the left testis was noted above to be larger in only 12 of 49 pairs it is evident that in this group, as in the group of pure species, there is a decided tendency for the left testis to be elongate in form as compared with the associated testis of the right side.

Four measurements on the relative length of the two testes of very young common pigeons are appended to table 8. All of these illustrate the point already mentioned in connection with table 2, namely, that at the time of hatching and for a short period thereafter the right testis is usually longer than the left.

TABLE 5
Measurements of testes of healthy young doves of pure species¹

NO.	DATE	LENGTH AND WIDTH	PER CENT OF DIFFERENCE	NO.	DATE	LENGTH AND WIDTH	PER CENT OF DIFFERENCE
A767	September 16	R = 6.2 L = 7.4	+ 19.3	E691	February 24	R = 4.7 x 1.3 L = 5.8 x 1.0	+ 23.4
E82	September 16	R = 7.3 L = 6.6	- 10.6	E512	February 24	R = 8.0 x 2.0 L = 8.3 x 2.0	+ 3.7
E31	September 16	R = 5.1 L = 4.7	- 8.5	E637	February 24	R = 5.0 x 1.0 L = 5.0 x 1.0	= 0.0
E37	October 14	R = 6.3 x 1.4 L = 6.2 x 1.4	- 1.6	E434	February 24	R = 5.0 x 1.8 L = 6.2 x 1.4	+ 24.0
E6	October 14	R = 5.5 x 1.7 L = 6.0 x 1.1	+ 9.1	E566	February 24	R = 4.7 x 1.2 L = 5.0 x 1.0	+ 6.4
E176	October 14	R = 7.1 x 1.9 L = 5.6 x 1.6	- 26.8	E503	February 24	R = 6.3 x 1.8 L = 6.4 x 1.5	+ 1.5
E217	October 14	R = 5.3 x 1.5 L = 6.1 x 1.4	+ 15.1	E465	February 24	R = 5.2 x 1.6 L = 4.9 x 1.4	- 6.1
E252	October 14	R = 6.4 x 1.9 L = 7.3 x 1.2	+ 14.1	E565	February 24	R = 4.5 x 1.1 L = 4.7 x 0.9	+ 4.4
E533	February 24	R = 6.0 x 1.6 L = 6.1 x 1.6	+ 1.6	E652	March 9	R = 5.3 x 1.2 L = 5.0 x 1.2	- 6.0

NO.	DATE	WEIGHT	PER CENT OF DIFFERENCE	LENGTH AND WIDTH	PER CENT OF DIFFERENCE
E685	February 24	R = 3.8 x 1.2 L = 5.0 x 1.0	+ 31.6	B469 March 9	R = 6.3 x 1.5 L = 6.9 x 1.2 + 9.5
E638	February 24	R = 5.0 x 1.0 L = 4.6 x 1.0	- 8.7	B456 March 9	R = 6.0 x 1.4 L = 5.4 x 1.3 - 10.0
E537	February 24	R = 6.7 x 1.8 L = 7.0 x 1.6	+ 4.5	E688 March 23	R = 6.2 x 1.7 L = 6.7 x 1.3 + 8.1
				E672 March 23	R = 5.5 x 1.1 L = 5.6 x 1.1 + 1.8
E458	April 12	R = 0.012 L = 0.011	- 9.1	6.9 x 2.0 6.9 x 1.5	= 0.0
E583	April 12	R = 0.010 L = 0.010	= 0.0	5.4 x 1.8 5.4 x 1.9	= 0.0
E643	April 12	R = 0.008 L = 0.007	- 14.3	5.2 x 1.9 5.7 x 1.4	+ 9.6
K401	April 20	R = 0.0050 L = 0.0045	- 11.1	5.5 x 1.3 5.3 1.1	- 3.7

¹ Some young of offspring of blond ring dove 'mutations' (?) are included in this list.

TABLE 6
Weights and measurements of testes of healthy adult common pigeons

NO.	DATE	WEIGHT	PER CENT OF DIFFERENCE	LENGTH AND WIDTH	PER CENT OF DIFFERENCE
A403	July 28, 1916	R = 0.975 L = 0.770	-26.6	19.0 20.3	+ 6.8
A492	July 28	R = 1.215 L = 1.425	+17.3	20.0 22.0	+10.0
A99	July 28	R = 0.825 L = 0.627	-31.6	20.0 17.8	-12.4
A57	May 31	R = 0.840 L = 0.890	+ 5.9	18.2 x 10.4 21.0 x 9.8	+15.4
B554	July 28	R = ——— L = ———		7.5 7.4	- 1.3
A485	July 30	R = 1.215 L = 1.010	-20.3	20.3 20.3	= 0.0
B407	July 30	R = 0.710 L = 0.900	+26.7	16.2 21.1	+30.2
A276	July 30	R = 0.925 L = 0.815	-13.5	18.0 16.8	- 7.1
B269	July 30	R = 0.790 L = 0.692	-14.2	19.3 20.5	+ 6.2
A58	August 2	R = 0.820 L = 0.690	-18.8	17.9 17.8	- 0.5
A321	August 2	R = 0.215 L = 0.930	+332.5	7.8 20.7	+165.4
O	August 2	R = 1.500 L = 0.980	-53.1	20.4 20.0	- 2.0
A319	August 2	R = 0.610 L = 0.685	+12.3	17.0 16.8	- 1.2
B664	November 10	R = 0.035 L = 0.029	-20.7	8.3 x 2.7 8.0 x 2.7	- 3.8

TABLE 6—*Continued*

NO.	DATE	WEIGHT	PER CENT OF DIFFERENCE	LENGTH AND WIDTH	PER CENT OF DIFFERENCE
B679	November 10	$\left\{ \begin{array}{l} R = 0.034 \\ L = 0.036 \end{array} \right.$	+ 5.9	$\begin{array}{l} 8.6 \times 2.8 \\ 8.0 \times 2.2 \end{array}$	- 7.5
B648	November 10	$\left\{ \begin{array}{l} R = 0.631 \\ L = 0.605 \end{array} \right.$	- 4.3	$\begin{array}{l} 19.2 \times 8.0 \\ 18.8 \times 7.5 \end{array}$	- 2.1
B637	November 10	$\left\{ \begin{array}{l} R = 0.035 \\ L = 0.030 \end{array} \right.$	- 16.6	$\begin{array}{l} 8.4 \times 2.3 \\ 8.0 \times 1.8 \end{array}$	- 5.0
B633	November 10	$\left\{ \begin{array}{l} R = 0.052 \\ L = 0.052 \end{array} \right.$	= 0.0	$\begin{array}{l} 8.8 \times 3.0 \\ 7.5 \times 2.8 \end{array}$	- 17.2
B641	November 10	$\left\{ \begin{array}{l} R = 0.045 \\ L = 0.037 \end{array} \right.$	- 21.6	$\begin{array}{l} 10.0 \times 2.6 \\ 8.5 \times 2.4 \end{array}$	- 17.6

TABLE 7

Weights and measurements of testes of healthy adult or adolescent common pigeons

NO.	DATE	WEIGHT	PER CENT OF DIFFERENCE	LENGTH AND WIDTH	PER CENT OF DIFFERENCE
B656	November 10	{ R = 0.380 L = 0.373	- 1.9	10.4 x 6.8 18.7 x 5.9	+79.8
A348	December 13	{ R = 0.724 L = 0.502	-44.2	18.7 x 8.8 19.5 x 6.8	+ 4.3
A292	December 13	{ R = 0.900 L = 0.768	-17.2	20.3 x 9.2 20.6 x 8.7	+ 1.4
A459	December 13	{ R = 0.080 L = 0.075	- 6.6	8.1 x 8.8 10.0 x 8.2	+23.4
E509	December 13	{ R = — L = —		9.4 x 2.6 8.0 x 1.5	-17.5
B555	December 13	{ R = 0.515 L = 0.448	-14.9	10.6 x 7.8 10.9 x 7.3	+ 2.8
A68	December 13	{ R = 0.836 L = 0.920	+10.0	19.0 x 9.5 19.5 x 9.3	+ 2.6
926	December 13	{ R = 0.616 L = 0.635	+ 3.1	18.2 x 7.4 19.1 x 7.1	+ 4.9
B510	December 13	{ R = 0.666 L = 0.492	-35.3	17.6 x 7.5 17.2 x 7.2	- 2.3
85	December 13	{ R = — L = —		15.2 x 6.4 12.3 x 6.6	-23.6
B515	December 13	{ R = 0.660 L = 0.645	- 2.3	18.1 x 7.4 19.0 x 7.7	+ 4.9
A171	December 13	{ R = 0.828 L = 0.660	-25.5	17.1 x 10.4 16.1 x 9.6	- 6.2
A104	December 13	{ R = 0.958 L = 0.845	-13.3	20.8 x 9.8 22.2 x 8.3	+ 6.7
B650	December 13	{ R = 0.205 L = 0.180	-13.9	12.7 x 5.0 12.6 x 4.5	- 0.8

TABLE 7—Continued

NO.	DATE	WEIGHT	PER CENT OF DIFFERENCE	LENGTH AND WIDTH	PER CENT OF DIFFERENCE
B513	December 13	{ R = 0.692 L = 0.650	— 6.4	18.0 x 9.0 19.7 x 8.3	+ 9.4
B642	December 13	{ R = 0.111 L = 0.075	—48.0	11.2 x 4.4 10.8 x 3.4	— 3.7
A243	December 13	{ R = 1.090 L = 0.812	—34.2	19.2 x 10.5 19.8 x 8.8	+ 3.1
193	December 13	{ R = 0.820 L = 0.610	—34.4	19.1 x 8.6 16.0 x 8.9	—19.3
B658	December 13	{ R = 0.248 L = 0.188	—31.9	12.2 x 6.6 11.1 x 5.3	+10.0
B502	March 9, 1917	{ R = 1.370 L = 1.050	—30.5	23.2 x 10.8 22.8 x 8.0	— 1.8

TABLE 8
Weights and measurements of testes of healthy adult common pigeons

NO.	DATE	WEIGHT	PER CENT OF DIFFERENCE	LENGTH AND WIDTH	PER CENT OF DIFFERENCE
B406	December 13	R = 0.485 L = 0.507	+ 4.5	16.9 x 8.2 18.7 x 6.4	+ 0.6
A306	December 13	R = 1.010 L = 0.802	-25.9	20.4 x 10.0 20.9 x 8.6	+ 2.4
Untag.	December 13	R = 1.130 L = 0.885	-27.7	23.2 x 9.6 21.2 x 8.6	- 9.4
A476	December 13	R = 1.187 L = 1.042	-13.9	23.6 x 10.6 22.0 x 9.0	- 7.3
A303	December 13	R = 0.525 L = 0.488	-7.6	18.6 x 7.8 16.5 x 7.5	-12.7
A454	December 13	R = 0.792 L = 0.878	+10.8	20.0 x 9.1 22.5 x 8.1	+12.5
B422	December 13	R = 0.574 L = 0.822	+43.2	18.0 x 7.3 19.6 x 8.6	+ 8.8
B651	December 13	R = 0.298 L = 0.280	- 6.4	16.3 x 5.2 15.8 x 5.3	- 3.1
A326	December 13	R = 0.532 L = 0.436	-22.0	17.8 x 6.4 16.6 x 6.5	- 7.2
B667	December 13	R = — L = —		6.5 x 2.0 6.8 x 1.7	+ 4.6
B511	December 13	R = 0.989 L = 0.753	-31.3	21.0 x 18.9 23.0 x 17.1	+ 9.5
A34	December 13	R = 0.263 L = 0.207	-26.5	8.5 x 5.9 8.1 x 5.3	- 4.9
A247	December 13	R = 0.490 L = 0.688	+40.4	17.2 x 7.4 20.0 x 7.8	+16.3
B655	December 13	R = 0.664 L = 0.390	-70.3	19.3 x 7.8 16.2 x 7.0	-19.1

TABLE 8—*Continued*

NO.	DATE ¹	LENGTH AND WIDTH	PER CENT OF DIFFERENCE
E411	December 13	R = 6.3 x 1.1 L = 5.6 x 1.0	-12.5
E547	December 13	R = 6.1 x 0.8 L = 5.8 x 1.0	- 5.1
E577	December 13	R = 6.1 x 1.0 L = 5.6 x 1.0	- 8.9
E552	December 13	R = 7.0 x 1.0 L = 5.0 x 1.0	-40.0

¹ The four individuals of this list were very young birds.

SIZE AND FORM OF TESTES OF DISEASED ADULT COMMON PIGEONS

Data can be supplied for only 6 individuals of this group. All of these (table 9) had smaller left testes. All left testes were also shorter than their right associates, but a comparison of the amounts (in per cent) of their shortness with the amounts (in per cent) of their size deficiency will show—as in other cases—that the left testes are the more elongate in form.

SIZE AND FORM OF TESTES OF HEALTHY ADULT SPECIFIC HYBRIDS

Complete weights and measurements for the testes of 18 individuals of this group are given in table 10. The left was larger in 2 cases and smaller in 16 cases. The number of 'reversals' of the usual size is not widely different from that noted in table 3 for pure species (2:22), but the indicated difference is in the same sense as found and reported in our earlier paper.

Although only two left testes of this group of 18 were as large as their associated rights, 14 of them were absolutely longer than their right associates. This group, therefore, like the two preceding groups, shows that the left testes of adults are decidedly more elongate than the right.

TABLE 9

Weights and measurements of testes of adult common pigeons dead of disease

NO.	DATE	DISEASE	WEIGHT	PER CENT OF DIFFERENCE	LENGTH AND WIDTH	PER CENT OF DIFFERENCE
A384	September 19	Crop (?)	$\left\{ \begin{array}{l} R = 0.050 \\ L = 0.037 \end{array} \right.$	-35.1	$\begin{array}{l} 7.8 \times 3.3 \\ 7.8 \times 2.6 \end{array}$	= 0.0
C-B9	November 22	Liver	$\left\{ \begin{array}{l} R = 0.578 \\ L = 0.496 \end{array} \right.$	-16.5	$\begin{array}{l} 17.5 \times 8.5 \\ 17.5 \times 7.7 \end{array}$	= 0.0
A266	November 22	Sp., body wall	$\left\{ \begin{array}{l} R = 0.027 \\ L = 0.019 \end{array} \right.$	-42.1	$\begin{array}{l} 6.4 \times 2.6 \\ 5.2 \times 2.8 \end{array}$	-23.1
A419	December 13	Liver	$\left\{ \begin{array}{l} R = 0.018 \\ L = 0.014 \end{array} \right.$	-28.5	$\begin{array}{l} 6.1 \times 2.4 \\ 6.0 \times 2.0 \end{array}$	-16.7
A425	January 28, 1917	old age (?)	$\left\{ \begin{array}{l} R = 0.170 \\ L = 0.068 \end{array} \right.$	-150.0	$\begin{array}{l} 11.1 \times 5.9 \\ 8.6 \times 4.0 \end{array}$	-29.1
A404	December 13	killed, jo., li.	$\left\{ \begin{array}{l} R = - \\ L = - \end{array} \right.$	-??	$\begin{array}{l} 9.3 \times 2.0 \\ 4.8 \times 2.1 \end{array}$	-93.8

TABLE 10
Weights and measurements of testes of healthy adult specific hybrids—killed April 11, 1917

NO.	WEIGHT	PER CENT OF DIFFERENCE	LENGTH AND WIDTH	PER CENT OF DIFFERENCE	NO.	WEIGHT	PER CENT OF DIFFERENCE	LENGTH AND WIDTH	PER CENT OF DIFFERENCE
A359	R = 0.828 L = 0.588	- 40.8	23.9 x 7.6 21.9 x 6.9	- 13.7	A364	R = 0.690 L = 0.628	- 9.9	21.2 x 7.5 23.3 x 6.5	+ 9.9
A458	R = 0.605 L = 0.643	+ 6.2	18.2 x 7.8 21.8 x 6.8	+ 19.8	A354	R = 0.602 L = 0.571	- 5.4	21.1 x 7.5 25.7 x 6.9	+ 21.8
A573	E = 0.710 L = 0.648	- 9.5	18.6 x 8.6 20.8 x 6.9	+ 11.8	A497	R = 0.748 L = 0.698	- 7.2	22.4 x 8.0 23.3 x 7.5	+ 4.0
B418	R = 0.540 L = 0.499	- 8.2	18.5 x 7.6 20.7 x 6.1	+ 11.9	A194	R = 0.933 L = 0.640	- 45.8	23.0 x 9.0 21.2 x 6.7	- 8.5
B328	R = 0.586 L = 0.572	- 2.4	17.0 x 8.0 21.0 x 7.0	+ 23.5	A562	R = 0.921 L = 1.015	+ 10.2	21.5 x 8.8 23.0 x 8.1	+ 6.9
A8	R = 0.720 L = 0.670	- 7.5	21.5 x 8.2 22.0 x 7.4	+ 2.3	B346	R = 0.684 L = 0.657	- 4.1	21.1 x 7.7 24.5 x 7.4	+ 16.1
A293	R = 0.883 L = 0.497	- 77.7 ¹	20.9 x 9.0 20.6 x 6.9	- 1.4	A245	R = 0.988 L = 0.825	- 19.7 ¹	23.8 x 8.1 28.4 x 7.7	+ 19.3
B285	R = 0.492 L = 0.373	- 31.9	19.8 x 6.3 20.7 x 5.0	+ 4.5	A365	R = 0.735 L = 0.592	- 24.2	20.3 x 8.5 21.4 x 6.5	+ 5.4
905	R = 0.712 L = 0.610	- 16.7	23.2 x 7.2 22.3 x 6.5	- 4.0	A628	R = 0.499 L = 0.438	- 13.9	15.8 x 7.7 18.3 x 5.7	+ 15.7

¹ These birds and the two following ones were killed April 18, 1917.

SIZE AND FORM OF TESTES OF DISEASED ADULT SPECIFIC
HYBRIDS

In tables 11 to 14 weights are given for 61 pairs of testes from diseased specific hybrids. Of this number 7 had larger left gonads; in 49 the right was the larger; and in 5 the two were of equal size. The number of larger lefts (reversals) is here hardly as large as in the group of pure species dead of disease. Touching this matter, however, is the fact that a very great majority of these hybrids were derived from two very closely related species—*St. alba* and *St. risoria*—and that the sex ratio is usually but little, if at all, affected by this cross. The very pronounced atrophy of both testes in disease—particularly in tuberculosis—is shown by these data to apply to this group equally with the groups previously examined.

The measurements of 58 pairs of testes show 38 longer and 18 shorter left testes. A comparison of the detailed measurements for the two testes of the birds listed in these same tables (11 to 14) will make it clear that here, as in other groups, the left testis is usually longer and thinner⁸ than the right.

THE FORM OF THE TWO TESTES IN HEALTHY YOUNG SPECIFIC
HYBRIDS

Measurements for 111 pairs of testes for birds of this group are given in tables 15, 16 and 17 (4 in table 2). At this immature stage (5 to 12 wks.) only about one-third (35:61) of the left testes have surpassed⁹ their right associates in length. In 19 of these 115 pairs a difference in length was not ascertainable.

⁸ In measuring the 'width' of the right and left testes the glands were measured (with Vernier calipers) at the widest point (usually anteriorly in the left testis) in their cross-wise dimension. The measurement of a third dimension was not attempted.

⁹ It was noted above that at the time of hatching the left testis is normally shorter than the right. It is only during post-natal development that the left becomes absolutely longer than the right. It is an interesting fact that the gonads of the male (ring doves) increase very little in size from the time of hatching to about the fourth month (compare tables 2 and 15 to 17). In the female, however, there is an early decrease in size (degeneration) of the right gonad, and a fairly steady increase in size of the left gonad.

TABLE II

Weights and measurements of testes of adult specific hybrids dead of disease¹

NO.	DATE	DISEASE	WEIGHT	PER CENT OF DIFF- ERENCE	LENGTH AND WIDTH	PER CENT OF DIFFER- ENCE
514	May 25, 1916	Sp., li.	{ R = 0.025 L = 0.255	+920.0	7.2 7.4	+ 2.8
109	June 8	Sp., li., me	{ R = 0.022 L = 0.018	-22.2		
A148	June 11	Sp., li.	{ R = 0.085 L = 0.069	-23.2	9.1 x 4.2 10.7 x 3.9	+17.6
B235	July 26	Liver, digest.	{ R = 0.012 L = 0.012	= 0.0	6.4 7.4	+15.6
190	August 1	Sp., li.	{ R = 0.040 L = 0.028	-42.9	8.2 7.8	-5.1
529	September 1	Sp., lu., li.	{ R = 0.083 L = 0.065	-27.7	9.0 x 4.5 10.3 x 3.6	+14.4
A168	September 5	Li. and sp.	{ R = 0.045 L = 0.041	- 9.7	8.4 x 3.3 9.4 x 2.9	+11.9
A389	September 5	Liver spleen	{ R = 0.570 L = 0.437	- 30.4		
749	September 10	Sp., liver	{ R = 0.026 L = 0.024	- 8.3	8.3 8.6	+3.6
551	September 20	Lungs	{ R = 0.075 L = 0.054	-38.8	9.7 x 3.8 9.9 x 2.9	+ 2.0
921	September 21	Li., sp., hem.	{ R = 0.069 L = 0.065	- 6.1	10.3 3.5 11.4 x 3.4	+10.7
107	September 24	Sp. and li.	{ R = 0.035 L = 0.033	- 6.1	8.5 x 2.7 8.0 x 2.7	- 6.3
A679	September 26	(Cause ?)	{ R = 0.097 L = 0.073	-32.8	11.0 x 4.5 12.3 x 3.3	+11.8
952	September 30	Sp., lu.; liver	{ R = 0.028 L = 0.021	-33.3		

TABLE 11—*Continued*

NO.	DATE	DISEASE	WEIGHT	PER CENT OF DIFF- ERENCE	LENGTH AND WIDTH	PER CENT OF DIFFER- ENCE
134	September 30	Sp., liver	{ R = 0.020 L = 0.019	— 5.3	6.9 x 2.4 8.4 x 2.1	+21.7
196	October 1	Sp., li.,	{ R = 0.030 L = 0.028	— 7.1	8.0 x 2.5 8.1 x 2.2	+ 1.3
930	October 5	Li. and sp.	{ R = 0.031 L = 0.025	—24.0	8.7 x 2.8 9.0 x 2.7	+ 3.4

TABLE 12

Weights and measurements of testes of adult specific hybrids dead of disease

NO.	DATE	DISEASE	WEIGHT	PER CENT OF DIFFER- ENCE	LENGTH AND WIDTH	PER CENT OF DIFFER- ENCE
A400	October 6	Sp., l; lu.,	{ R = 0.045 L = 0.035	-28.6	9.2 x 3.0 10.5 x 2.3	+14.1
77	October 7	digest. (?)	{ R = 0.321 L = 0.247	-29.9	15.4 x 6.3 15.3 x 5.1	- 0.7
A35	October 7	Li., sp., lu.	{ R = 0.050 L = 0.042	-19.0	9.4 x 2.9 12.1 x 2.6	+28.7
127	October 7	Sp.	{ R = 0.028 L = 0.020	-40.0	8.1 x 3.0 8.0 x 2.3	- 1.3
504	October 12	Old age	{ R = 0.057 L = 0.050	-14.0	9.9 x 3.5 11.4 x 3.4	+15.2
A520	October 13	Liver (?)	{ R = 0.236 L = 0.255	+ 8.1	15.9 x 5.5 14.9 x 5.6	- 6.7
A163	October 20	Sp., li.	{ R = 0.037 L = 0.031	-19.3	9.0 x 2.5 9.0 x 2.5	= 0.0
520	November 15	Sp., R. lu., li.	{ R = 0.038 L = 0.035	- 8.6	8.4 x 3.0 9.5 x 2.6	+13.1
950	November 16	Sp., li., lu.	{ R = 0.036 L = 0.031	-16.1	9.2 x 3.0 8.6 x 2.8	- 6.9
592	November 21	Sp., li., lungs (?)	{ R = 0.377 L = 0.345	- 9.3	16.5 x 7.0 18.4 x 6.4	+11.5
A94	November 26	Sp., li., intes.	{ R = 0.022 L = 0.020	-10.0	7.8 x 2.5 8.0 x 2.2	+ 2.6
A42	December 6	Li., lu., sp.	{ R = 0.014 L = 0.014	= 0.0	6.4 x 2.0 5.4 x 2.2	-18.5
B264	December 10	Digest. (?)	{ R = 0.035 L = 0.027	-29.6	8.4 x 3.0 9.2 x 2.2	+ 9.5
102	December 13	Sp., li.	{ R = 0.020 L = 0.023	+15.0	6.7 x 2.3 8.4 x 2.4	+25.4

TABLE 12—*Continued*

NO.	DATE	DISEASE	WEIGHT	PER CENT OF DIFFER- ENCE	LENGTH AND WIDTH	PER CENT OF DIFFER- ENCE
538	December 17	Sp.	{ R = 0.031 L = 0.025	-24.0	9.0 x 2.4 7.7 x 2.6	-16.9
509	December 18	Sp. and li.	{ R = 0.028 L = 0.030	+ 7.1	7.1 x 2.9 6.4 x 3.2	-10.9
533	December 20	Lu., sp., me.	{ R = 0.028 L = 0.023	-21.7	6.0 x 2.7 7.4 2.5	+23.3

TABLE 13

Weights and measurements of testes of adult specific hybrids dead of disease

NO.	DATE	DISEASE	WEIGHT	PER CENT OF DIFFER- ENCE	LENGTH AND WIDTH	PER CENT OF DIFFER- ENCE
78	December 26	Liver	{ R = 0.061 L = 0.052	-17.3	10.0 x 3.0 9.7 x 2.9	- 3.0
A133	December 29	Sp. and li.	{ R = 0.012 L = 0.012	= 0.0	7.3 x 2.0 6.4 x 2.1	-14.1
200	December 29	Sp., lu., li.	{ R = 0.018 L = 0.017	- 5.9	8.6 x 2.1 8.0 x 2.2	- 7.5
957	January 2	Sp., li.	{ R = 0.034 L = 0.026	-30.8	7.8 x 3.0 7.4 x 2.5	- 5.4
92	January 2	Li., sp.	{ R = 0.035 L = 0.030	-16.7	8.3 x 2.9 8.7 x 2.8	+ 4.8
928	January 6	Sp., li.	{ R = 0.022 L = 0.018	-22.2	7.3 x 2.4 8 x 2.4 (?)	+ 9.6
A695	January 10	Li. sp.	{ R = 0.315 L = 0.279	-12.9	15.1 x 6.8 15.6 x 5.7	+ 3.3
953	January 19	Sp., lu., li.	{ R = 0.032 L = 0.024	-33.3	7.5 x 3.0 8.1 x 2.3	+ 8.0
A192	February 3	Li., sp., jo.	{ R = 0.023 L = 0.018	-27.7	7.6 x 2.4 6.8 x 2.2	-11.8
A189	February 17	Killed	{ R = 0.062 L = 0.048	-29.1	9.3 x 3.5 8.7 x 3.0	- 6.9
A322	February 24	Sp., li., jo.	{ R = 0.038 L = 0.035	- 8.6	7.8 x 3.2 7.9 x 2.5	+ 1.3
904	February 27	Sp., li.	{ R = 0.031 L = 0.025	-24.0	8.2 x 2.5 8.2 x 2.3	= 0.0
E551	March 4	Hemorrh.(juv.)	{ R = 0.023 L = 0.019	-21.0	5.9 x 1.8 4.8 x 1.5	-20.8

TABLE 13—*Continued*

NO.	DATE	DISEASE	WEIGHT	PER CENT OF DIFFER- ENCE	LENGTH AND WIDTH	PER CENT OF DIFFER- ENCE
A181	March 8	Li., sp., lu.	{ R = 0.037 L = 0.025	-48.0	9.0 x 3.0 7.4 x 2.3	-21.6
A141	March 10	Sp., lu., liver	{ R = 0.043 L = 0.042	- 2.4	10.4 x 3.6 11.3 x 3.1	+ 8.6
A153	March 17	Li., sp.	{ R = 0.035 L = 0.035	= 0.0	8.5 x 3.1 10.0 x 2.4	+17.6
536	March 18	Li., sp., lu., me.	{ R = 0.045 L = 0.039	-15.4	7.2 x 2.8 9.8 x 2.4	+36.1

TABLE 14

Weights and measurements of testes of adult specific hybrids dead of disease

NO.	DATE	DISEASE	WEIGHT	PER CENT OF DIFFER- ENCE	LENGTH AND WIDTH	PER CENT OF DIFFER- ENCE
45	March 22	Throat	{ R = 0.394 L = 0.250	-49.6	16.0 x 6.4 15.3 x 5.2	- 4.5
B399	March 22	Too much salt (?)	{ R = 0.360 L = 0.377	+ 4.7	16.9 x 6.3 17.9 x 6.0	+ 5.9
A284	March 22	Too much salt (?)	{ R = 0.612 L = 0.565	- 8.2	18.2 x 7.9 21.1 x 7.5	+15.9
126	March 22	Sp., li.	{ R = 0.043 L = 0.045	+ 4.6	8.9 x 3.0 9.3 x 3.4	+ 4.5
A568	March 23	(Cause ?)	{ R = 0.545 L = 0.423	-28.8	18.7 x 7.3 18.8 x 6.6	+ 0.5
526	March 27	Sp., li.	{ R = 0.062 L = 0.050	-24.0	10.2 x 3.0 12.5 x 2.6	+22.5
E508	March 23	Healthy (?) salt	{ R = 0.067 L = 0.044	-52.3	8.9 x 3.5 9.2 x 2.8	+ 3.3
B322	April 8	Sp., li., hem.	{ R = 0.052 L = 0.060	+15.4	10.3 x 2.6 12.3 x 3.1	+19.4
945	April 8	Sp., li.	{ R = 0.034 L = 0.031	- 9.7	7.4 x 3.0 8.4 x 2.9	+13.5
A252	April 23	Sp., li.	{ R = 0.025 L = 0.025	= 0.0	7.0 x 2.9 8.1 x 2.6	+15.7

TABLE 15
Measurements of testes of healthy young specific hybrids

NO.	DATE	LENGTH	PER CENT OF DIFFERENCE	NO.	DATE	LENGTH AND WIDTH	PER CENT OF DIFFERENCE
E56	September 16	R = 5.0 L = 6.0	+ 20.0	B602	September 16	R = 6.6 L = 6.8	+ 3.0
E30	September 16	R = 5.0 L = 5.0	= 0.0	E183	September 16	R = 5.0 L = 5.0	= 0.0
E163	September 16	R = 6.0 L = 6.0	= 0.0	E76	September 16	R = 7.0 L = 6.1	- 14.7
A880	September 16	R = 5.0 L = 5.4	+ 8.0	E320	October 14	R = 5.1 x 1.0 L = 4.7 x 1.4	- 8.5
E35	September 16	R = 4.5 L = 5.7	+ 26.6	E380	October 14	R = 4.6 x 1.7 L = 5.3 x 1.6	+ 15.2
A862	September 16	R = 5.0 L = 6.1	+ 22.0	E305	October 14	R = 4.8 x 1.0 L = 4.9 x 0.9	+ 2.1
E39	September 16	R = 4.6 L = 4.6	= 0.0	B499	October 14	R = 6.4 x 1.0 L = 5.4 x 1.0	- 18.5
E157	September 16	R = 6.5 L = 5.4	- 20.4	B500	October 14	R = 5.5 x 1.2 L = 5.2 x 1.1	- 5.8
E71	September 16	R = 5.8 L = 5.4	- 7.4	E328	October 14	R = 4.2 x 1.4 L = 5.0 x 0.9	+ 18.9
E212	September 16	R = 5.2 L = 5.8	+ 11.5	E341	October 14	R = 5.6 x 1.4 L = 4.7 x 1.0	- 19.1

E46	September 16	{	R = 6.4 L = 5.7	- 12.3	E326	October 14	{	R = 6.2 x 1.3 L = 5.5 x 1.1	- 12.7
O	September 16	{	R = 16.1 L = 18.0	+ 11.8	E256	October 14	{	R = 6.8 x 1.1 L = 5.6 x 1.2	- 21.4
F230	September 16	{	R = 5.6 L = 4.6	- 21.7	E332	October 14	{	R = 6.4 x 1.0 L = 5.1 x 1.0	- 25.5
E245	September 16	{	R = 6.8 L = 4.7	- 44.7	B441	October 14	{	R = 6.4 1.0 L = 4.6 x 1.0	- 39.1
E158	September 16	{	R = 6.6 L = 5.6	- 17.9	E174	October 14	{	R = 7.0 x 1.3 L = 6.2 x 1.3	- 12.9
E96	September 16	{	R = 5.6 L = 4.7	- 19.1	E200	October 14	{	R = 6.4 x 1.8 L = 5.5 x 1.6	- 16.3
E95	September 16	{	R = 4.3 L = 5.4	+ 25.5	E369	October 14	{	R = 5.5 1.0 L = 5.0 x 0.9	- 10.0
E107	September 16	{	R = 5.2 L = 5.5	+ 5.8	E312	October 14	{	R = 5.2 x 0.9 L = 4.9 x 1.0	- 6.1

TABLE 16
Measurements of testes of healthy young specific hybrids

NO.	DATE	LENGTH AND WIDTH	PER CENT OF DIFFERENCE	NO.	DATE	LENGTH AND WIDTH	PER CENT OF DIFFERENCE
E207	October 14	{ R = 5.2 x 1.1 L = 5.0 x 0.9	- 4.0	E378	November 10	{ R = 7.2 x 1.3 L = 6.6 x 1.0	- 9.1
E166	October 14	{ R = 5.2 x 1.1 L = 5.3 x 1.1	+ 1.9	E510	November 10	{ R = 4.6 x 1.0 L = 4.0 x 1.0	- 15.0
E394	October 14	{ R = 5.5 x 1.2 L = 5.1 x 1.2	- 7.8	E343	November 10	{ R = 5.0 x 1.0 L = 5.0 x 0.9	= 0.0
E307	October 14	{ R = 4.8 x 1.3 L = 4.8 x 1.1	= 0.0	E501	November 10	{ R = 5.0 x 0.9 L = 4.9 x 0.7	- 2.0
E179	October 14	{ R = 5.0 x 1.0 L = ... x 1.0	?	E462	November 10	{ R = 5.2 x 1.4 L = 5.7 x 1.1	+ 9.6
E303	October 14	{ R = 4.4 x 1.1 L = 5.4 x 1.1	+ 22.7	E492	November 10	{ R = 4.9 x 1.5 L = 4.9 x 1.1	= 0.0
E348	October 14	{ R = 4.8 x 1.0 L = 5.0 x 1.0	+ 4.2	B436	November 10	{ R = 6.2 x 1.4 L = 4.6 x 1.3	- 3.5
B434	October 14	{ R = 4.9 1.0 L = 5.2 x 1.0	+ 6.1	E143	November 10	{ R = 6.0 x 1.0 L = 5.3 x 1.0	- 13.2
E184	October 14	{ R = 5.0 x 1.3 L = 4.9 x 1.1	- 2.0	E334	November 10	{ R = 5.5 x 1.0 L = 6.3 x 1.0	+ 14.5

E40	October 14	{	R = 4.5 x 1.3 L = 4.5 x 0.9	= 0 0	E514	November 10	{	R = 4.5 x 0.8 L = 5.0 x 0.8	+ 11.1
E221	October 14	{	R = 5.5 x 1.3 L = 4.8 x 1.2	- 14.6	E449	November 10	{	R = 4.5 x 1.2 L = 4.3 x 1.0	- 4.6
E140	October 14	{	R = 5.1 x 1.4 L = 5.6 x 1.3	+ 9.8	E482	November 10	{	R = 4.9 x 0.9 L = 5.4 x 0.9	+ 10.2
E88	October 14	{	R = 5.0 x 0.8 L = 4.8 x 0.9	- 4.1	E396	November 10	{	R = 4.9 x 1.6 L = 6.5 x 1.3	+ 32.6
E180	October 14	{	R = 4.5 x 1.0 L = 4.8 x 1.0	+ 6.7	E454	November 10	{	R = 6.0 x 1.0 L = 4.8 x 0.9	- 25.0
E94	October 14	{	R = 6.2 x 1.2 L = 5.9 x 1.3	- 5.1	E193	November 10	{	R = 6.4 x 1.5 L = 5.0 x 1.5	- 28.0
E270	October 14	{	R = 5.1 x 1.3 L = 5.7 x 1.0	+ 11.7	F99	November 10	{	R = 6.4 x 1.2 L = 5.0 x 1.4	- 28.0
E260	October 14	{	R = 6.0 x 1.2 L = 6.0 x 1.0	= 0.0	E519	November 10	{	R = 5.4 x 1.0 L = 5.0 x 0.9	- 8.0

TABLE 17
Measurements of testes of healthy young specific hybrids

NO.	DATE	LENGTH AND WIDTH	PER CENT OF DIFFERENCE	NO.	DATE	LENGTH AND WIDTH	PER CENT OF DIFFERENCE
E478	November 10	R = 4.4 x 1.2 L = 5.0 x 1.2	+ 13.6	B471	February 24	R = 5.5 x 1.3 L = 5.5 x 1.3	= 0.0
E429	November 10	R = 7.5 x 0.9 L = 5.8 x 1.0	- 29.3	E621	February 24	R = 5.7 x 1.2 L = 4.8 x 1.5	- 18.7
E463	November 10	R = 4.7 x 1.2 L = 4.7 x 1.2	= 0.0	E623	February 24	R = 6.4 x 1.2 L = 5.6 x 1.1	- 14.3
E210	November 10	R = 6.7 x 1.2 L = 7.3 x 1.0	+ 8.9	E618	February 24	R = 5.0 x 1.0 L = 3.4 x 0.9	- 47.0
E387	November 10	R = 4.8 x 1.4 L = 4.8 x 1.1	= 0.0	B470	February 24	R = 5.0 x 1.0 L = 4.3 x 1.0	- 16.3
E489	December 12	R = 6.0 x 1.1 L = 4.7 x 1.0	- 27.7	B435	February 24	R = 4.8 x 1.0 L = 4.5 x 1.4	- 6.7
E513	December 12	R = 6.4 x 0.7 L = 6.0 x 0.8	- 6.6	E487	March 9	R = 5.1 x 0.8 L = 5.1 x 0.8	= 0.0
E560	December 12	R = 4.8 x 0.9 L = 4.1 x 0.9	- 17.1	E677	March 9	R = 4.7 x 0.9 L = 4.8 x 0.8	+ 2.1
E527	December 12	R = 5.3 x 1.0 L = 4.3 x 0.9	- 23.2	E695	March 9	R = 4.7 x 0.9 L = 4.6 x 0.9	- 2.2
E609	December 12	R = 6.5 x 1.1 L = 6.0 x 1.0	- 8.3	E700	March 9	R = 5.4 x 0.9 L = 5.6 x 0.9	+ 3.7

E521	December 12	{	R = 4.2 x 1.1 L = 4.9 x 1.0	+ 16.6	E964	March 9	{	R = 5.0 x 1.0 L = 4.9 x 1.0	- 2.0
E467	December 12	{	R = 5.9 x 0.8 L = 5.8 x 0.9	- 1.7	E669	March 9	{	R = 3.9 x 1.0 L = 4.1 x 1.0	+ 5.1
E469	December 12	{	R = 4.7 x 1.0 L = 5.0 x 1.1	+ 6.4	E645	March 9	{	R = 4.8 x 1.0 L = 4.8 x 1.0	= 0.0
E428	December 12	{	R = 5.2 x 0.9 L = 5.6 x 0.7	+ 7.7	K319	March 9	{	R = 5.2 x 1.0 L = 5.2 x 1.0	= 0.0
E657	February 24	{	R = 4.8 x 0.8 L = 4.8 x 0.8	= 0.0	E662	March 9	{	R = 5.1 x 1.2 L = 5.1 x 0.9	= 0.0
B466	February 24	{	R = 5.3 x 1.3 L = 4.4 x 1.2	- 20.4	K320	March 9	{	R = 5.9 x 0.9 L = 5.3 x 0.9	- 11.3
B458	February 24	{	R = 5.6 x 1.1 L = 5.1 x 1.0	- 9.8	E591	March 9	{	E = 5.1 x 0.9 L = 4.1 x 0.8	- 24.4
E687	March 9	{	R = 4.9 x 0.9 L = 4.9 x 0.9	= 0.0	K351	March 23	{	R = 4.4 x 0.9 L = 4.5 x 0.9	+ 2.3
E681	March 9	{	R = 4.9 x 1.2 L = 3.6 x 1.0	- 36.1	K397	March 23	{	R = 5.1 x 0.9 L = 3.9 x 0.9	- 30.9
E404	March 9	{	R = 6.1 x 0.8 L = 4.3 x 0.8	- 41.9	K399	March 23	{	R = 4.8 x 1.0 L = 4.9 x 1.0	+ 2.1
K391	March 23	{	R = 5.7 x 0.9 L = 5.6 x 0.9	- 1.8	K381	March 23	{	R = 4.7 x 0.8 L = 4.7 x 0.8	= 0.0

SIZE AND FORM OF TESTES OF HEALTHY ADULT TRI-SPECIFIC HYBRIDS

The group of birds here described as tri-specific hybrids all involve the same three species—*St. alba*, *St. risoria*, *St. douraca*. They are rather closely related species. *Alba* and *risoria* have been considered as varieties only by several writers; and *douraca* seems to have been considered by Stejeneger as the wild representative of the semi-domesticated *risoria*. The tabulated data indicate—by the relatively few cases of larger left testes (size-reversals)—that this group more closely approximates to the conditions found in pure species than do the other groups (common pigeons, specific hybrids, generic hybrids) investigated.

Tables 18, 19 and 20 supply the data obtained from 69 pairs of testes. Only 6 left testes were the larger, 61 were smaller, and 2 were the size equivalents of the other member of the pair. On the other hand, 42 left testes were longer and only 24 were shorter than the right; in three cases the two organs were of equal length.

FORM OF TESTES IN HEALTHY YOUNG TRI-SPECIFIC HYBRIDS

Measurements for 44 pairs of testes are given in table 21 (4 in table 2). The left was the longer in 20 pairs. The details of the table show further that the left testis is usually thinner—of less width (proportionately less wide) than the right.

SIZE AND FORM OF TESTES OF HEALTHY ADULT GENERIC HYBRIDS

A group of 35 healthy generic hybrids were killed for the purposes of this study.¹⁰ Here the left testis was larger in 10 cases, smaller in 24, and of equal size in 1 case (tables 22, 23). The number of larger left testes (reversals) is clearly quite out of proportion to that found in any of the preceding groups of birds;

¹⁰ The principal crosses involved here are: *Streptopelia* × *Turtur*; *Spilopelia* × *Streptopelia*; *Zenaidura* × *Zenaidura*; *Stigmatopelia* × *Streptopelia*. Two or three individuals of a sub-family cross involving *Zenaidura*-*Zenaidura* × *Streptopelia* are also included in the tabulated data. In the summarized data of table 28 (detailed weights and measurements not given), to be mentioned later, two family hybrids, *Columba* × *Streptopelia*, are included.

in those groups the width of the cross involved was either less in extent or wholly absent. These figures, then, strongly confirm the impression (p. 102) obtained from the "diseased generic hybrids" reported upon in our earlier paper. This impression being that "the number of the exceptions (reversals) seems to increase with the degree of hybridization (width of the cross)."

The left testis is here longer than its associate in a very high proportion of cases—24: 8; in 2 cases the compared lengths were equal.

The form of the testes of healthy young generic hybrids may be noted in this connection. The 19 pairs (1 is in table 2) of testes of table 24 show 8 longer and 9 shorter left testes and 2 pairs of equal length. Of these, 5 are clearly larger; 7 are smaller.

FORM AND SIZE OF TESTES IN DISEASED ADULT GENERIC HYBRIDS

The weights of 14 pairs of testes of diseased generic hybrids are recorded in table 25. The left testis was larger in 9 cases, smaller in 4, and of equivalent size in 1 case. The numbers are not large, but it is clear that similar proportions of larger (reversed) left testes are found in none other of the groups considered—neither in the present nor in the earlier report on this subject. The only group that approximates to these proportions is this same group—diseased generic hybrids—of our earlier report. The ratio there of larger lefts to larger rights was 7:12. In 10 of the 14 pairs of testes recorded here the left was the longer; in three pairs the left was shorter, and in one pair there was no difference in length.

After all of the data that has just been discussed had been gathered, tabulated and described (in the form found in the preceding pages), it was decided to accumulate a third set of data on this subject. Since the number of weights obtained for some of the bird groups is smaller—both in our earlier communication and in the data thus far treated here—than is desirable, it was thought well to learn whether similar proportions for the various groups would be found in a third collection of data. That the proportions found in the two earlier sets do reappear in these

TABLE 13
Weights and measurements of testes of healthy adult or adolescent tri-specific hybrids—killed March 23, 1917

NO.	WEIGHT	PER CENT OF DIFFERENCE	LENGTH AND WIDTH	PER CENT OF DIFFERENCE	NO.	WEIGHT	PER CENT OF DIFFERENCE	LENGTH AND WIDTH	PER CENT OF DIFFERENCE
A768 {	R = 0.585 L = 0.482	- 21.4	20.5 x 6.2 19.7 x 6.2	- 4.0	E559 {	R = 0.376 L = 0.355	- 5.9	18.0 x 6.1 18.0 x 5.9	= 0.0
E306 {	R = 0.518 L = 0.475	- 9.0	17.8 x 6.6 19.8 x 5.7	+ 11.2	B586 {	R = 0.430 L = 0.760	+ 76.7	17.9 x 6.0 24.4 x 6.6	+ 36.3
E507 {	R = 0.085 L = 0.066	- 28.8	11.0 x 2.9 10.0 x 2.8	- 10.0	A665 {	R = 0.430 L = 0.360	- 19.4	16.0 x 7.0 16.2 x 6.2	+ 1.3
A730 {	R = 0.770 L = 0.670	- 14.9	20.6 x 7.5 22.5 x 6.6	+ 9.2	E138 {	R = 0.572 L = 0.510	- 12.1	19.0 x 6.6 17.0 x 7.0	- 11.8
E178 {	R = 0.740 L = 0.545	- 35.8	18.8 x 7.8 18.6 x 6.4	- 1.1	E272 {	R = 0.388 L = 0.267	- 45.3	15.2 x 5.9 14.4 x 5.0	- 5.5
E382 {	R = 0.528 L = 0.377	- 40.0	20.6 x 7.2 22.4 x 5.3	+ 8.7	E5 {	R = 0.540 L = 0.478	- 12.9	20.3 x 6.4 20.0 x 6.5	- 1.5
E357 {	R = 0.430 L = 0.290	- 48.3	16.4 x 5.8 16.9 x 5.0	+ 3.0	A294 {	R = 0.550 L = 0.455	- 20.9	18.3 x 7.2 23.8 x 5.7	+ 30.1
E444 {	R = 0.240 L = 0.170	- 41.2	15.5 x 4.9 14.6 x 4.1	- 6.2	B589 {	R = 0.580 L = 0.443	- 30.9	20.5 x 7.1 18.2 x 7.2	- 12.6
A702 {	R = 0.635 L = 0.480	- 32.3	19.2 x 7.9 21.4 x 6.4	+ 11.5	E57 {	R = 0.685 L = 0.465	- 47.3	22.4 x 7.6 20.4 x 6.3	- 9.8
E403 {	R = 0.488 L = 0.365	- 33.7	18.3 x 6.6 20.2 x 6.1	+ 10.4	E254 {	R = 0.610 L = 0.420	- 45.2	23.1 x 7.2 21.4 x 5.8	- 7.9

A673	{ R = 0.500 L = 0.438	- 14.1	17.5 x 6.4 18.9 x 6.6	+ 8.0	{ E364	R = 0.522 L = 0.430	- 21.4	17.3 x 7.3 19.1 x 5.8	- 10.4
E289	{ R = 0.500 L = 0.385	- 29.9	17.2 x 7.2 16.9 x 5.6	- 1.8	{ A827	R = 0.830 L = 0.530	- 56.6	22.1 x 8.5 20.2 x 8.3	- 9.4
E347	{ R = 0.490 L = 0.415	- 18.1	16.3 x 6.1 17.3 x 5.2	+ 6.1	{ E170	R = 0.250 L = 0.160	- 56.2	14.9 x 5.3 13.9 x 3.7	- 7.2
A318	{ R = 0.535 L = 0.513	- 4.3	20.5 x 6.7 21.5 x 6.4	+ 4.9	{ B573	R = 0.673 L = 0.485	- 38.8	21.7 x 7.3 19.0 x 6.3	- 14.2
A859	{ R = 0.835 L = 0.628	- 32.9	22.2 x 8.5 21.5 x 8.3	- 3.2	{ 977	R = 0.452 L = 0.330	- 36.9	16.6 x 7.3 18.0 x 6.0	+ 8.4
E360	{ R = 0.071 L = 0.036	- 97.2	10.8 x 3.4 9.3 x 2.8	- 16.1	{ E225	R = 0.320 L = 0.225	- 42.2	17.0 x 6.0 15.2 x 5.1	- 11.8
E128	{ R = 0.738 L = 0.668	- 10.5	21.5 x 8.0 22.0 x 7.2	+ 2.3	{ A531	R = 0.693 L = 0.560	- 23.8	19.1 x 7.8 20.6 x 6.7	+ 7.8
E242	{ R = 0.578 L = 0.400	- 44.5	21.1 x 7.3 20.1 x 5.8	- 4.9	{ E50	R = 0.650 L = 0.498	- 30.5	21.6 x 7.1 21.3 x 5.8	- 1.4
E105	{ R = 1.032 L = 0.944	- 9.3 ¹	22.0 x 8.6 23.5 x 8.3	+ 6.8	{ A810	R = 0.705 L = 0.640	- 10.1 ¹	21.0 x 7.9 22.1 x 7.3	+ 5.2
A691	{ R = 0.598 L = 0.559	- 6.9	19.0 x 7.7 23.1 x 6.0	+ 21.5	{ B265	R = 0.721 L = 0.695	- 3.7	21.5 x 7.8 22.6 x 6.9	+ 5.1

¹ This and following bird killed April 20, 1917.

TABLE 19
Weights and measurements of healthy adult or adolescent tri-specific hybrids—killed March 23, 1917

NO.	WEIGHT	PER CENT OF DIFFERENCE	LENGTH AND WIDTH	PER CENT OF DIFFERENCE	NO.	WEIGHT	PER CENT OF DIFFERENCE	LENGTH AND WIDTH	PER CENT OF DIFFERENCE
B649 {	R = 0.460 L = 0.312	- 47.4	19.4 x 6.8 17.3 x 5.3	- 12.1	E171 {	R = 0.369 L = 0.369	= 0.0	18.0 x 5.9 16.7 x 5.9	- 7.8
E77 {	R = 0.360 L = 0.388	+ 7.7	16.9 x 6.2 18.6 x 6.1	+ 10.1	A813 {	R = 0.799 L = 0.608	- 31.4	21.0 x 8.4 22.3 x 7.7	+ 6.2
E438 {	R = 0.390 L = 0.390	= 0.0	16.7 x 6.1 17.3 x 6.8	+ 3.6	E344 {	R = 0.370 L = 0.388	+ 4.9	15.3 x 6.5 18.0 x 6.3	+ 17.6
E466 {	R = 0.006 L = 0.004	- 50.0	5.0 x 2.0 5.0 x 1.4	= 0.0	E188 {	R = 0.435 L = 0.328	- 32.6	22.0 x 6.3 22.1 x 5.4	+ 0.4
E442 {	R = 0.016 L = 0.014	- 14.3	6.6 x 2.0 6.3 x 2.0	- 4.7	A844 {	R = 0.557 L = 0.490	- 13.6	18.6 x 7.5 20.0 x 6.8	+ 7.5
A758 {	R = 0.560 L = 0.448	- 25.0	21.3 x 7.0 21.4 x 5.7	+ 0.5					

TABLE 20

Weights and measurements of testes of healthy adult or adolescent tri-specific hybrids

NO.	DATE	WEIGHT	PER CENT OF DIFFERENCE	LENGTH AND WIDTH	PER CENT OF DIFFERENCE
A865	March 9	$\left\{ \begin{array}{l} R = 0.805 \\ L = 0.740 \end{array} \right.$	- 8.8	$\begin{array}{l} 23.5 \times 7.7 \\ 24.3 \times 6.6 \end{array}$	+ 3.4
E189	March 9	$\left\{ \begin{array}{l} R = 0.632^* \\ L = 0.542 \end{array} \right.$	-16.6	$\begin{array}{l} 20.5 \times 7.4 \\ 23.4 \times 6.4 \end{array}$	+14.1
E329	March 9	$\left\{ \begin{array}{l} R = 0.153 \\ L = 0.130 \end{array} \right.$	-17.7	$\begin{array}{l} 11.7 \times 4.0 \\ 13.2 \times 3.5 \end{array}$	+12.8
E376	March 9	$\left\{ \begin{array}{l} R = 0.650 \\ L = 0.457 \end{array} \right.$	-42.2	$\begin{array}{l} 19.7 \times 7.7 \\ 21.5 \times 6.4 \end{array}$	+ 9.1
E340	March 9	$\left\{ \begin{array}{l} R = 0.507 \\ L = 0.616 \end{array} \right.$	+21.5	$\begin{array}{l} 21.6 \times 6.7 \\ 23.3 \times 6.5 \end{array}$	+ 7.9
E20	March 9	$\left\{ \begin{array}{l} R = 0.695 \\ L = 0.557 \end{array} \right.$	-24.8	$\begin{array}{l} 21.9 \times 7.6 \\ 22.1 \times 6.4 \end{array}$	+ 0.9
E271	March 9	$\left\{ \begin{array}{l} R = 0.295 \\ L = 0.290 \end{array} \right.$	- 1.7	$\begin{array}{l} 12.2 \times 5.3 \\ 17.1 \times 4.8 \end{array}$	+40.0
E391	March 9	$\left\{ \begin{array}{l} R = 0.571 \\ L = 0.483 \end{array} \right.$	-18.2	$\begin{array}{l} 20.0 \times 7.1 \\ 21.6 \times 5.8 \end{array}$	+ 8.0
E393	March 9	$\left\{ \begin{array}{l} R = 0.318 \\ L = 0.353 \end{array} \right.$	+11.0	$\begin{array}{l} 16.9 \times 5.6 \\ 19.1 \times 5.6 \end{array}$	+13.0
E11	March 9	$\left\{ \begin{array}{l} R = 0.670 \\ L = 0.623 \end{array} \right.$	- 7.5	$\begin{array}{l} 21.2 \times 8.9 \\ 21.2 \times 6.9 \end{array}$	= 0.0
E269	March 23	$\left\{ \begin{array}{l} R = 0.520 \\ L = 0.435 \end{array} \right.$	-19.5	$\begin{array}{l} 20.3 \times 6.1 \\ 18.2 \times 5.7 \end{array}$	-11.5
E126	March 23	$\left\{ \begin{array}{l} R = 0.656 \\ L = 0.420 \end{array} \right.$	-56.2	$\begin{array}{l} 19.4 \times 6.7 \\ 20.2 \times 6.4 \end{array}$	+ 4.1
B639	March 23	$\left\{ \begin{array}{l} R = 0.725 \\ L = 0.852 \end{array} \right.$	+17.5	$\begin{array}{l} 21.4 \times 7.6 \\ 24.9 \times 7.6 \end{array}$	+16.3
A801	March 23	$\left\{ \begin{array}{l} R = 0.640 \\ L = 0.620 \end{array} \right.$	- 3.2	$\begin{array}{l} 18.0 \times 6.7 \\ 21.9 \times 7.1 \end{array}$	+21.7
A868	March 23	$\left\{ \begin{array}{l} R = 0.790 \\ L = 0.655 \end{array} \right.$	-20.6	$\begin{array}{l} 19.5 \times 8.3 \\ 21.8 \times 6.4 \end{array}$	+11.8
E16	March 23	$\left\{ \begin{array}{l} R = 0.410 \\ L = 0.365 \end{array} \right.$	-12.3	$\begin{array}{l} 10.4 \times 6.0 \\ 11.4 \times 6.0 \end{array}$	+ 9.6
A705	March 23	$\left\{ \begin{array}{l} R = 0.500 \\ L = 0.405 \end{array} \right.$	-23.4	$\begin{array}{l} 22.6 \times 7.0 \\ 23.5 \times 6.0 \end{array}$	+ 3.9
A623	March 23	$\left\{ \begin{array}{l} R = 0.774 \\ L = 0.648 \end{array} \right.$	-19.4	$\begin{array}{l} 18.2 \times 8.3 \\ 20.6 \times 7.6 \end{array}$	+13.2

TABLE 21
Measurements of testes of healthy young tri-specific hybrids

NO.	DATE	LENGTH AND WIDTH	PER CENT OF DIFFERENCE	NO.	DATE	LENGTH AND WIDTH	PER CENT OF DIFFERENCE
A237	September 16	R = 6.3 L = 4.9	- 28.6	B464	February 24	R = 6.3 x 1.1 L = 5.1 x 1.1	- 23.5
E304	October 14	R = 6.1 x 1.0 L = 4.5 x 1.1	- 35.5	E470	February 24	R = 4.7 x 1.4 L = 6.2 x 1.9	+ 31.9
E315	October 14	R = 5.3 x 1.3 L = 4.3 x 1.2	- 23.3	E658	February 24	R = 6.8 x 1.0 L = 4.3 x 1.2	- 58.1
E308	October 14	R = 6.9 x 1.3 L = 6.7 x 1.3	- 2.9	E505	February 24	R = 4.7 x 1.2 L = 5.0 x 1.1	+ 6.4
E87	October 14	R = 5.8 x 1.4 L = 5.4 x 1.4	- 7.4	E648	March 9	R = 7.5 x 1.1 L = 7.5 x 1.1	= 0.0
E280	October 14	R = 5.7 x 1.1 L = 4.2 x 1.2	- 35.7	E673	March 9	R = 5.5 x 1.1 L = 4.6 x 1.1	- 19.5
E351	October 14	R = 6.4 x 0.9 L = 4.2 x 0.9	- 52.4	E660	March 9	R = 5.2 x 1.2 L = 5.3 x 1.2	+ 1.9
E137	October 14	R = 4.5 x 1.0 L = 5.0 x 1.0	+ 11.1	E696	March 9	R = 5.1 x 1.0 L = 4.9 x 1.0	- 4.1
E524	December 12	R = 5.2 0.8 L = 8.7 0.8	+ 67.3	E570	March 9	R = 6.1 x 0.9 L = 4.6 x 1.0	- 32.6
E606	December 12	R = 5.3 x 1.3 L = 5.4 x 0.9	+ 1.9	E440	March 9	R = 8.1 x 3.2 L = 8.2 x 2.7	+ 1.2

E544	February 24	{ R = 5.4 x 1.3 L = 5.5 x 1.1	+ 1.8	E581	March 9	{ R = 4.7 x 1.2 L = 4.8 x 1.1	+ 2.1
B482	February 24	{ R = 5.0 x 1.0 L = 5.0 x 1.0	= 0.0	E496	March 9	{ R = 6.0 x 2.0 L = 6.0 x 2.0	= 0.0
E576	February 24	{ R = 6.2 x 2.1 L = 6.2 x 2.0	= 0.0	E426	March 9	{ R = 10.1 x 3.2 L = 9.1 x 2.7	- 10.9
E530	February 24	{ R = 6.8 x 1.8 L = 5.9 x 1.4	- 15.3	E409	March 9	{ R = 7.0 x 2.0 L = 6.9 x 2.0	- 1.4
E455	February 24	{ R = 6.2 x 1.8 L = 7.0 x 1.5	+ 12.9	E626	March 9	{ R = 5.8 x 2.8 L = 5.9 x 2.8	+ 1.7
E529	February 24	{ R = 5.2 x 1.1 L = 5.1 x 1.2	+ 1.9	E586	March 9	{ R = 6.6 x 1.8 L = 5.7 x 1.5	- 15.8
E413	February 24	{ R = 7.6 x 1.8 L = 7.0 x 1.1	- 8.6	E497	March 9	{ R = 6.0 x 2.0 L = 6.2 x 1.9	+ 3.3
E491	February 24	{ R = 4.4 x 1.3 L = 5.0 x 1.0	+ 13.6	E589	March 23	{ R = 8.3 x 2.8 L = 8.9 x 2.8	+ 7.2
E671	March 9	{ R = 4.3 x 0.9 L = 4.4 x 0.9	+ 2.3	E494	March 23	{ R = 8.8 x 4.4 L = 6.5 x 3.6	- 35.4
E594	March 9	{ R = 4.6 x 1.1 L = 4.6 x 1.1	= 0.0	E186	March 23	{ R = 6.5 x 2.0 L = 5.4 x 2.0	- 20.4
E678	March 9	{ R = 4.7 x 1.0 L = 4.6 x 1.0	- 2.2	K315	March 23	{ R = 5.1 x 0.8 L = 5.8 x 0.8	+ 13.7
E589	March 23	{ R = 8.3 x 2.8 L = 8.9 x 2.8	+ 7.2	K419	April 20	{ R = 6.1 x 1.0 L = 6.3 x 0.9	+ 3.3

TABLE 22

Weights and measurements of testes of healthy adult generic hybrids

NO.	KILLED	WEIGHT	PER CENT OF DIFFERENCE	LENGTH AND WIDTH	PER CENT OF DIFFERENCE
265	June 2	{ R = 0.496 L = 0.400	-24.0	17.2 x 8.1 18.2 x 6.4	+ 5.8
979	March 23	{ R = 0.402 L = 0.355	-13.2	16.3 x 6.7 18.8 x 6.5	+15.3
A229	March 23	{ R = 0.533 L = 0.695	+30.3	19.2 x 8.1 21.4 x 8.0	+11.4
A172	March 23	{ R = 0.395 L = 0.395	= 0.0	15.6 x 7.0 18.1 x 5.5	+16.0
A221	March 23	{ R = 0.643 L = 0.530	-21.3	19.2 x 7.8 19.8 x 7.2	+ 3.1
A25	March 23	{ R = 0.310 L = 0.340	+ 9.7	15.4 x 6.6 broken	?
A327	March 23	{ R = 0.715 L = 0.660	- 8.3	15.4 x 7.8 14.6 x 6.8	- 5.5
B267	March 23	{ R = 0.660 L = 0.558	-18.2	20.6 x 7.8 22.4 x 7.3	+ 8.7
911	March 23	{ R = 0.053 L = 0.058	+ 9.4	8.0 x 3.0 9.0 x 3.2	+12.5
A232	March 23	{ R = 0.455 L = 0.477	+ 4.9	16.4 x 7.0 18.0 x 7.0	+ 9.7
A299	March 23	{ R = 0.395 L = 0.304	-29.9	16.8 x 6.6 17.8 x 6.3	+ 5.9
A175	March 23	{ R = 0.440 L = 0.409	- 7.6	17.2 x 7.3 20.2 x 6.4	+17.4
A170	March 23	{ R = 0.620 L = 0.518	-19.7	21.2 x 7.4 21.4 x 7.2	+ 0.9
B350	March 23	{ R = 0.464 L = 0.471	+ 1.5	18.5 x 7.2 22.3 x 5.8	+20.6
A375	April 12	{ R = 0.684 L = 0.471	-45.2	19.6 x 7.7 19.6 x 6.9	= 0.0
A682	April 12	{ R = 0.600 L = 0.480	-25.0	19.2 x 7.7 19.2 x 6.2	= 0.0
E423	April 20	{ R = 0.632 L + 0.638	+ 0.9	23.5 x 6.5 23.2 x 6.6	- 1.3

TABLE 23
Weights and measurements of testes of healthy adult generic hybrid doves—killed April 18, 1917

NO.	WEIGHT	PER CENT OF DIFFERENCE	LENGTH AND WIDTH	PER CENT OF DIFFERENCE	NO.	WEIGHT	PER CENT OF DIFFERENCE	LENGTH AND WIDTH	PER CENT OF DIFFERENCE
A224 {	R = 0.435 L = 0.350	- 24.3	13.9 x 7.6 14.6 x 6.9	+ 5.1	B227 {	R = 0.347 L = 0.352	+ 1.4	15.3 x 6.2 15.2 x 6.5	- 0.6
B202 {	R = 0.418 L = 0.353	- 18.4	15.5 x 7.5 18.4 x 6.2	+ 18.7	E274 {	R = 0.371 L = 0.338	- 9.7	14.6 x 6.9 15.4 x 6.3	+ 5.5
A398 {	R = 0.350 L = 0.325	- 7.7	16.1 x 6.3 18.6 x 5.2	+ 15.5	940 {	R = 0.558 L = 0.540	- 3.3	19.9 x 7.0 23.7 x 6.8	+ 19.1
B203 {	R = 0.285 L = 0.254	- 12.2	11.9 x 6.7 13.2 x 5.7	+ 10.9	E59 {	R = 0.615 L = 0.995	+ 61.8	18.5 x 7.9 24.1 x 8.3	+ 30.3
A300 {	R = 0.435 L = 0.352	- 23.6	14.0 x 7.7 15.0 x 6.4	+ 7.1	B288 {	R = 0.905 L = 0.806	- 12.2	21.0 x 8.7 18.6 x 8.1	- 12.9
A627 {	R = 0.605 L = 0.357	- 69.4	18.9 x 7.1 16.1 x 5.9	- 17.4	A618 {	R = 0.483 L = 0.391	- 23.5	18.4 x 6.3 19.8 x 5.3	+ 7.6
E261 {	R = 0.137 L = 0.148	+ 8.0	10.4 x 9.6 12.3 x 9.4	+ 18.2	B266 {	R = 0.310 L = 0.248	- 25.0	13.6 x 6.0 13.3 x 6.0	- 2.3
918 {	R = 0.388 L = 0.325	- 19.4	16.4 x 6.5 14.1 x 6.2	- 16.3	933 {	R = 0.473 L = 0.345	- 37.1	15.7 x 6.9 14.6 x 6.9	- 7.4
A608 {	R = 0.581 L = 0.530	- 9.6	18.6 x 7.9 21.0 x 6.4	+ 12.9	E275 {	R = 0.030 L = 0.032	+ 6.7	7.6 x 2.6 7.7 x 2.6	+ 1.3

TABLE 24
Measurements of test-s of healthy young generic hybrids

NO.	DATE	LENGTH AND WIDTH	PER CENT OF DIFFERENCE	NO.	DATE	LENGTH AND WIDTH	PER CENT OF DIFFERENCE
E223	September 16	R = 5.5 L = 5.2	- 5.8	E427	February 24	R = 6.7 x 1.4 L = 6.5 x 1.5	+ 3.1
A879	October 14	R = 7.1 x 2.1 L = 6.8 x 1.6	- 4.4	B486	February 24	R = 4.6 x 1.0 L = 5.4 x 1.1	+ 17.4
E239	October 14	R = 7.5 x 1.2 L = 7.7 x 1.1	+ 2.6	E655	February 24	R = 4.6 x 1.7 L = 4.7 x 1.4	+ 2.1
E314	October 14	R = 4.5 x 1.0 L = 5.2 x 0.9	- 15.5	E511	March 9	R = 6.1 x 1.0 L = 6.2 x 0.9	+ 1.6
E371	October 14	R = 4.8 x 1.0 L = 4.6 x 0.9	- 4.3	E634	March 9	R = 5.2 x 1.1 L = 5.0 x 1.2	- 4.0
E421	November 10	R = 4.9 x 1.0 L = 3.8 x 0.8	- 28.9	E517	March 9	R = 6.3 x 1.7 L = 6.4 x 1.6	+ 1.6
E540	December 12	R = 6.8 x 1.0 L = 6.6 x 1.2	- 3.0	K313	March 9	R = 4.2 x 0.8 L = 4.2 x 0.8	= 0.0
A277	December 12	R = 5.5 x 1.4 L = 6.0 x 1.7	+ 9.1	E596	March 23	R = 4.1 x 0.7 L = 5.2 x 0.7	+ 26.8
E419	December 12	R = 5.5 x 1.4 L = 4.9 x 1.1	- 12.2	K322	March 23	R = 5.5 x 0.4 L = 4.1 x 0.5	- 34.1

TABLE 25

Weights and measurements of testes of adult generic hybrids dead of disease

NO.	DATE	DISEASE	WEIGHT	PER CENT OF DIFFER- ENCE	LENGTH AND WIDTH	PER CENT OF DIFFER- ENCE
881	May 25	Liver and spleen	{ R = 0.365 L = 0.310	-17.7	17.2 x 6.2 14.9 x 6.2	-15.4
443	June 8	Sp., li., me.	{ R = 0.035 L = 0.037	+ 5.7	7.1 x 3.1 7.1 x 3.1	= 0.0
888	September 16	Sp., li., peri- card.	{ R = 0.210 L = 0.215	+ 2.4	13.7 x 5.5 15.3 x 5.4	+11.6
375	October 6	Hemorrhage	{ R = 0.324 L = 0.441	+ 3.6	17.2 x 6.0 21.5 x 5.7	+25.0
773	October 15	Sp., li.	{ R = 0.016 L = 0.019	+18.7	6.6 x 2.1 6.7 x 2.0	+ 1.5
253	October 15	Old age ?	{ R = 0.063 L = 0.067	+ 6.3	9.0 x 3.8 10.0 x 3.8	+11.1
522	October 16	(Cause ?)	{ R = 0.018 L = 0.020	+11.1	6.4 x 2.2 6.8 x 2.3	+ 6.3
207	November 9	Sp., liver	{ R = 0.090 L = 0.098	+ 8.9	8.8 x 5.5 10.0 x 4.8	+13.6
466	December 5	Li., lu., sp.	{ R = 0.015 L = 0.018	+20.0	5.5 x 2.4 4.4 x 2.8	-25.0
599	February 10	Sp., li.	{ R = 0.054 L = 0.050	- 8.0	7.6 x 2.3 7.7 x 2.5	+ 1.3
A363	February 14	Sp., li.	{ R = 0.377 L = 0.300	-25.6	17.6 x 6.0 16.8 x 5.7	- 4.7
A88	February 25	Sp., liver	{ R = 0.027 L = 0.028	+ 3.7	7.1 x 2.3 7.8 x 2.3	+ 9.8
B391	March 7	Sp.	{ R = 0.027 L = 0.027	= 0.0	6.6 x 1.9 7.6 x 1.8	+15.1
A17	March 25	Sp., lu.	{ R = 0.037 L = 0.031	-19.3	8.0 x 3.7 10.0 x 2.5	+25.0

data, collected between May 1 and October 25, is shown by the summary¹¹ given in table 28.

The numbers concerned in this summary are smaller than those found in tables (summaries) 1 and 26. They include weighings of only 102 pairs of testes. But here, as in both of those groups of data, it is found that: (a) The healthy birds of pure species show fewest larger left testes (reversals); (b) the generic hybrids (widest cross) show most reversals; and (c) specific hybrids and tri-specific hybrids show intermediate numbers of reversals. Of the birds dead of disease, the generic hybrids again show the greatest proportion of reversals. The common pigeons are second in this respect.

There are available, therefore, three separate accumulations of data on the effect of degree of hybridity—or width of cross—on the number of size reversals of the two testes; these would seem to establish the fact that the number of these reversals increases with the width of the cross. This fact becomes of much significance when joined with two other facts. These are, first, that a male dove which bears testes ‘reversed’ in the order of their size, is like a female and unlike a normal male in this respect; for, in the female the left ovary is always the larger ovary, and is normally the only gonad to persist beyond an early point in life. The second fact is that it is in these same generic (and family) crosses where, by the wide cross, males can be made to arise from female-producing eggs. Finally, the three facts stand in such relations as to give support to the conclusion elsewhere stated by the writer, that the sex of doves and pigeons has been experimentally controlled. The testes measurements of the generic hybrids indicate, as do other lines of study, that a bird whose sex has been reversed usually retains one or another identifiable characteristic of the opposite sex; that is to say, such an adult is likely in some manner to betray the initial sex tendency of the germ from which it arose. In the present case, the gonads of the male may assume the size relations of the female.

¹¹ It is thought that sufficient details of the weights and measurements are supplied by the preceding tables. Measurements were made of only a part of this group of gonads and these too are omitted from the table.

TABLE 26

Classified summary of weights and measurements of testes

CLASS	STATE	WEIGHT RELATIONS			LENGTH RELATIONS		
		L +	L =	L -	L +	L =	L -
Pure species.....	Healthy (young).....	0	1	3	17	4	10
	Healthy (adult).....	2	0	22	17	0	7
	Diseased (adult).....	3	4	13	10	1	8
	Total.....	5	5	38	44	5	25
Tri-specific hybrids ¹	Healthy (young).....				20	5	23
	Healthy (adult).....	6	2	61	42	3	24
	Total.....	6	2	61	62	8	47
Specific hybrids.....	Healthy (young).....				35	19	61
	Healthy (adult).....	2	0	16	14	0	4
	Diseased (adult).....	7	5	49	38	2	18
	Total.....	9	5	65	87	21	83
Common pigeons.....	Healthy (young).....				0	0	4
	Healthy (adult).....	12	1	36	25	1	27
	Diseased (adult).....	0	0	6	0	2	4
	Total.....	12	1	42	25	3	35
Generic hybrids.....	Healthy (young).....				8	2	9
	Healthy (adult).....	10	1	24	24	2	8
	Diseased (adult).....	9	1	4	10	1	3
	Total.....	19	2	28	42	5	20
Total healthy adult		32	4	159	122	6	70
Total diseased adult		19	10	72	58	9	33
Grand total (+ juv.).....		51	15	234	260	42	210

¹ Closely related species (see text).

TABLE 27
Condensed summary of previous and present data¹

CLASS	RATIO: L+ : L-	STATE	WEIGHT RELATIONS			LENGTH RELATIONS		
			L+	L	L-	L+	L	L-
Pure species.....	1: 15.0	Healthy.....	2	1	30	34	5	21
		Diseased.....	12	10	44	24	3	10
	1: 5.3	Total.....	14	11	74	58	8	31
Common pigeons.....	1: 3.7	Healthy.....	17	1	63	26	1	31
		Diseased.....	2	0	14	2	0	14
	1: 4.5	Total.....	19	1	77	28	1	45
Specific hybrids.....	1: 4.4	Healthy.....	8	7	35	57	25	72
		Diseased.....	17	15	73	52	3	22
	1: 4.3	Total.....	25	22	108	109	28	94
Generic hybrids.....	1: 2.4	Healthy.....	10	1	24	32	4	17
		Diseased.....	16	1	16	12	2	9
	1: 1.5	Total.....	26	2	40	44	6	26
Total healthy.....			37	10	152	149	35	141
Total diseased.....			47	26	147	90	8	55
Grand total.....			84	36	299	239	43	196

¹ All weights and measurements for tri-specific hybrids are omitted. These were not represented in the earlier data which are here combined with the data of the present paper. Of these tri-specific hybrids data are available for 'healthy' birds only; the ratio of L+ : L- is 1: 10.2, while this ratio for pure species is 1: 15.0. The three species involved (in nearly all of this group of hybrids) are very closely related ones (as noted elsewhere).

TABLE 28

Additional classified weight relations of testes of pigeons, dead or killed between May 1 and October 25, 1917 (after all the birds of the preceding tables; the individual weights and lengths are omitted)

CLASS	STATE	WEIGHT RELATIONS		
		L +	L =	L -
Pure species.....	Healthy (adult or adol.).....	1	3	10
	Diseased (adult).....	3	3	8
Specific hybrids.....	Healthy (adult or adol.).....	2	6	15
	Diseased (adult).....	1	4	17
Tri-specific hybrids...	Healthy (adult).....	1	0	4
	Diseased (adult).....	0	1	2
Common pigeons.....	Diseased (adult).....	2	2	4
Generic hybrids.....	Healthy (adult or adol.).....	1	1	3
	Diseased (adult).....	3	2	3
Totals (102 birds)		14	22	66

SUMMARY

The conclusions of our earlier paper on the normal size relations of the right and left testes of pigeons are confirmed by much more extensive data. In healthy adult doves and pigeons the right testis is larger than the left in a very high percentage of cases. The left testis, in a high percentage of cases, is absolutely longer and thinner—more nearly the shape of the single persistent (left) ovary of the female—than is the right testis; it is relatively longer and thinner in probably nearly all cases.

The other conclusions of the earlier paper are also confirmed:

- The left testis more nearly approaches the shape which is characteristic of the 'single' left ovary than does the right.
- In disease—particularly in tuberculosis—the testes undergo extreme atrophy (often 90 to 95 per cent); the reduction is greater in the right than in the left testis; the ovary probably suffers no reduction whatever.

Further investigation has shown that the right testis of very young (embryo to few weeks) squabs, contrary to the situation in the adults, is normally longer than the left.

The single (persistent) left ovary of young female squabs is twice or more than twice as long as is either testis borne by males of similar age (3 to 7 weeks).

In hybrids the normal size relations of the two testes is disturbed; the sex ratio is also disturbed in hybrids (see first citation under note 4). Some hybrid males bear gonads whose size relations are those of normal females; and the disturbance of the sex ratio in hybrid birds is known to consist in the production of an excess of males. These facts are probably interrelated.

The number of hybrid males which exhibit gonads with the size relations 'reversed' (or, as in the normal female) increases as the width of the cross from which the hybrids originate increases. The excess of males from such crosses in birds is known to increase similarly (see first citation under note 4).

Disproportionately large numbers of males with reversed size relations of the gonads have been found among generic hybrids of doves and pigeons. The generic crosses which produced these hybrids yield the greatest excess of males. The application of the principle stated here to the several individual cases of generic hybrids, whose origin from female-producing eggs is otherwise suspected, will be made in a full and complete account of our studies on the control of sex in pigeons. The results support the conclusion that sex has been controlled in these forms, and that a male which is forced to arise from a female-producing egg may show in the relative size of its gonads an approximation to the relative size of the gonads of a female.

A PROBABLE CASE OF SUPERFETATION IN THE COW¹

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Recently the writer (Harman, '17) reported a case of superfetation in the cat.² Since that time a student of hers has called attention to a condition in the cow which may be interpreted as superfetation.³ A brief account of it follows.

A cow owned by Mr. Reppert was mated on December 22, 1917. After she was taken away from the bull, she was kept in a small lot, and there was certainly no opportunity for a second mating until May 15, 1917, when she was removed from the lot to the pasture. In fact, there was hardly a probability that copulation could have occurred. However, for a short time she was with a number of other cattle in a pasture, but no males were among them. On September 27, 1917, she gave birth to a heifer calf, normally developed and slightly above the average in size. On October 1, she gave birth to another calf, which, according to the decision of the veterinarian, was a little more than a four months' fetus. This second calf was inclosed in the amnion and the placenta was in good condition. The calf was dead when it was born, but had the appearance of having been dead for only a very short time, as there was no indication of decay. During pregnancy the cow seemed to be normal in every way, having a normal appetite and gave milk up until about six weeks before the birth of the first calf. After the birth of the

¹ Contribution from the Zoological Laboratory, Kansas State Agricultural College, no. 21.

² Harman, Mary T. A case of superfetation in the cat. *Anat. Rec.*, vol. 13, no. 3.

³ I wish to express my indebtedness to Mr. R. R. Reppert, a graduate student, for calling my attention to this case and for giving me the data concerning it.

first calf the milk flow was good, and the birth of the second calf was a surprise to the man in charge.

Certainly there was in the uterus at the same time two embryos of widely different degrees of development. Whether or not the second embryo began its development after the first one or simultaneously with it is a problem. It seems, however, that if it should be a case of retardation of development the placenta would have given evidence of a lack of blood supply, or the embryo would have shown some degree of decay from having been dead for a long time. The embryo seemed normal. If it was a case of superfetation, the only chance for a second copulation was at the time that the cow was removed to the pasture, which was a little more than four months from the time of the birth of the last calf. If a second copulation did not take place, and if the eggs were not fertilized at the same time, there must have been a retention of spermatozoa, in the female reproductive organs, as was suggested by Sumner.⁴ Also, there must have been either an ovulation during pregnancy, or, as was suggested by Harman, '17, the egg was retained in the reproductive organs of the female for a length of time before fertilization. Whether or not this case may be interpreted as a true case of superfetation, or as a case of retarded development, it adds another one to the list of mammals in which the uterus contained embryos of widely different degrees of development at the same time.

⁴ Sumner, F. B. 1916 Notes on the superfetation and defertilization among mice. *Biol. Bull.*, vol. 30.

SUPPLEMENT

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DARWINISM AND NATIONS*

MAYNARD M. METCALF

I had thought to ask your attention at this time to some new data which throw light upon the origin of the *Ciliata*, but the suggestion has been made that the various scientific societies, in their meetings, give some attention to problems connected with the great task the Nation has before it in the present war. I have therefore changed my plan and shall speak upon the theme "Darwinism and Nations."

Standing as we do in the midst of this great war, we are too near it to see its issues in their true relation and in proper perspective. Yet a few things stand out so boldly that they may be seen without much danger of confusion and false estimate. They challenge our attention and must be faced and thoughtfully appraised. There is taking place before us a gigantic experimental demonstration in social life, and students of the evolution of society have such opportunity as has rarely been presented to see great forces in strenuous action molding the future of mankind. The truth or falsity of certain claims as to human relations and the evolution of the life of man must surely be made more clear than ever before.

We as zoologists are still further challenged to consider the present phenomena by the strictly biological form in which the

* Address of the President of the American Society of Zoologists at the Fifteenth Annual Meeting of that Society, December 27, 1917, Minneapolis, Minnesota.

argument of the protagonists of the Central Powers is so often put. German students, more than any others, have carried Darwinism to its logical extreme, with an unhesitating, uncompromising quality that is in itself admirable. The Nageli-Weismann conception of the continuity of the germ-plasm and the consequent non-heritability of acquired characters marked a decided advance in our thinking upon evolution and problems of human progress. It furnished a necessary foundation for studies in genetics and is vital in questions of eugenics which may in time be the central questions of human society. The fact that German scholars are not now taking an important part in studies of genetics should not obscure for us the fact of the great debt geneticists owe to Weismann and his fellow countrymen.

Human individuals in their endeavor to perpetuate themselves are subject to selection under three forms—natural selection, marriage selection, and social selection dependent upon castes or cliques. The latter two, marriage selection and social selection, are chiefly intranational and do not apply to rivalries between those groups of men we call nations. Natural selection, on the other hand, applies to nations as well as individuals, and German thinkers are right in emphasizing it, though not to the exclusion of all other considerations.

Germany's presentation of her national philosophy and her claims for herself among the nations is too complex for any brief adequate statement, but we may note a number of its salient features:—

Nations, like individuals, are subject to natural selection through the struggle for existence. This struggle must take in large measure the form of war.

In this struggle it is the strong that survive and only the strong deserve to survive.

A nation therefore should conserve and increase its strength in order to take its proper place upon the Earth.

The Germans are the mightiest and the greatest race and nation, and no considerations should be allowed to stand in the way of their taking their rightful place as the dominant people. The struggle for existence between nations must not be ameliorated but must be allowed to take its full and natural course in order that Germany, mightiest

of nations, may reach undisputed dominance. Any considerations that would hamper the outworking of this most fundamental law of nature are contrary to nature and so immoral. It is natural and therefore is right that the most mighty should come to unrestricted, unhampered rule.

In order to thrust herself forward most effectively in the struggle for existence the nation must do whatever is best for the development of her might. Everything that tends to this end is right; everything that hinders is wrong. The state, perfect in her power, is the ultimate goal and no considerations beyond the state are to be entertained. The state is a law unto herself. She is the source of all law and so is above all law.

I have tried to give a very moderate statement of these items from Germany's presentation of her claims. By quotations from Treitschke, Bernhardt, von Bülow, Harnack and many others I could have put each item in much more extreme form, but understatement will do little harm for our present purpose.

Several friends to whom I have read this paper urge me to include the actual citations without paraphrase, and after some consideration I have decided to do this at the close of the paper. The actual words are so vivid that I fear if they were introduced at this point they would render difficult dispassionate consideration of the ideas we are discussing.

The German argument is in general logical. It presents a philosophy of national life and relations which accepts the Darwinian principle to the full and applies it uncompromisingly. If the premises are correct, I see no escape from the conclusions. But logic has no necessary relation to truth. We have conspicuous examples of eminent logicians who have failed to convince. Herbert Spencer is such an one. His reasoning is keen, but he seems so to enjoy the processes of his argument that he hastens to them without taking time to scrutinize the premises upon which his reasoning is based, and he is not convincing. The zoologist may think him quite an astronomer; the astronomer may regard him as well founded in geology; the geologist may think him profound in his knowledge of biology; but few students have the highest regard for Spencer as a thinker in their own special fields. In his "Philosophy of Style," on the other hand, where his data seem sound, his conclusions are convincing.

That logic and factual truth have no necessary relation is clearly shown in mathematics, the purest of pure logic. Mathematics, like all logic, is occupied solely with truth of relation and not at all with truth of fact. Indeed whole fields of mathematics confessedly deal with data falsely assumed. It seems strange that mathematics should ever be classed as a science. Science deals with phenomena, mathematics, and all logic, deal only with relation.

But pardon this digression. We started upon it, I believe, from the statement that the uncompromising logic of the German philosophy is no sufficient indication of its truth unless it be founded upon true data. Shall we examine from this point of view some of the statements and implications in the German argument, with the purpose of bringing out some of the fundamental relations between groups in human society and some of the fundamental elements in national strength, all of course from the point of view of the evolution of mankind and of society?

"Nations, like individuals, are subject to natural selection through the struggle for existence." Yes, surely. But this is not a statement of the whole truth. Like individuals, nations can, if they wish, supercede natural selection in large measure by developing cooperation, the principle that obtains to a greater or less degree among all communal organisms. Human communities, especially, have freed their members from much of the stress of the struggle for existence, by substituting cooperation for rivalry in a very large proportion of the individual relations within the group. Interdependence between the individuals of the group has been so developed, through cooperation and division of labor, that cooperation may perhaps fairly be said to transcend natural selection as an influence upon the life of highly civilized man. The higher the development of human society, the more dominant becomes the principle of cooperation. Only in the most primitive communities can there be an approach to unrestricted natural selection. Indeed we know today no such human societies, and it is probable that this stage of social evolution was already passed before man's ancestors became truly men.

Not only has human society today substituted cooperation for natural selection, in large measure. We are beginning to see more clearly the biological and social possibilities in eugenics, and future human society is altogether likely to relegate into desuetude the *laissez faire* principle of unrestricted selection among men.

As between individuals, so also between groups, between nations, it is possible to substitute cooperation for selection to a very considerable degree, and the question of the desirable extent of such substitution is one of the most important of social problems.

"In the struggle for existence it is the strong that survive and only the strong deserve to survive." Again yes, but we must carefully definite the word strong as here used. We need to remember not only the point just made, that rivalry is not the only principle and that cooperation and rivalry are coordinate principles in international relations. We must remember as well that national strength cannot be assumed to be only physical might or such power as is useful in unrestricted rivalry. Other forms of strength, strength of character, moral strength, strong emotional sympathies, a genuine sympathetic kindly feeling toward all sorts and conditions and races of men and an ability to understand them and their points of view, may tend to promote cooperation and may well be the greatest assets of a nation physically and intellectually sound. This may well be the type of national character toward which we must move in order to reach such international relations as will bring man to his fullest development. Humanness, with a degree of natural humility, an ingrained altruism, may be the culminating quality in that strength which is most real and effective.

"A nation should conserve and increase its might in order to take its proper place upon the Earth." Yes, but here again might needs defining. Physical and spiritual strength both need to be considered.

"The Germans are the mightiest and the greatest race and nation, and no consideration should be allowed to stand in the way of their taking their rightful place as the dominant people."

In developed power in a military way, including that organization of the people which is necessary to give the fullest support to the army and navy, Germany surely led the world. Of her potential power, compared to that of the British Empire, France, America, or Russia, we must speak with less confidence. But with all her developed military strength, Germany has shown a surprising spiritual difference from other peoples, and this somewhat unique character needs scrutiny in making any estimate of her national power. To this point we will return.

Her philosophy of the state as the world unit, her teaching that the state is ultimate and that duty to the state is the final duty, her claim that the state is the source of all law and is therefore above all law and not subject to it, is based upon assumptions that need examination.

It might be possible to organize world society upon the basis of the nations as rival rather than cooperating units, but such a plan consistently carried out would give not world society but international anarchy, at least until such time as one state should have become sovereign for the whole world. Just as in all smaller social communities selection is ameliorated by cooperation, and as intracommunal society is possible only in so far as cooperation is developed, so between nations world society is possible only to the extent to which cooperation is developed. Within the community rivalry has been restricted and controlled and the struggle between individuals restrained by the development of law. Cooperation between the individuals of the community, and not the dominance of a single individual, is the plan of organization that has developed in all human communities, and the degree of development of cooperation and restraint of struggle seems a fair measure of the advancement of the civilization of the community. It might be possible to have a group of human beings among whom the freedom of the struggle was unrestricted. This probably would lead to the complete dominance of one individual in each group. But human social evolution has not taken this direction. Communities of almost this type are found among some of the gregarious feral *Ungulata*, but not among men.

It is difficult to see any reason for believing that such a relation between nations would be possible for the world as a whole and would work out for human welfare. The presumption seems to favor a world society organized upon much the same plan as that which has everywhere developed in and between lesser communities, that is, a community of nations, with highly developed cooperation and with the violence of rivalry restricted by law founded upon sanctions of moral and physical force by the whole community of nations. The evolution of human society has been moving in this direction and recent events seem to be greatly accelerating such development. The German conception of the nation as the ultimate unit, with unrestricted struggle for survival between these several national units, until one becomes dominant and absorbs the others, seems to be contrary to the whole current of social evolution, and its realization seems most improbable.

If a world community, and not the individual state, is the ultimate unit of social cooperation, of course the German conception of the state as the ultimate source of all law is false, the ultimate source of all enacted law being really the world community of nations, and the ultimate sanctions of such law being world sanctions, not national sanctions.

Let us further consider this point so frankly and so strongly urged by recent German social philosophers, namely that the state, being the ultimate source of law, is itself above all law. There are two great assumptions in this statement, and each deserves examination:—first, that the state is the ultimate source of law; second, that as it is itself the source of law it is above the law and not subject to it. Both statements I believe to be fallacious. Even leaving out of account the thought of a world community and its laws, the German conception of the state as the source of law is partial and inadequate. The state is the mechanism for enacting law and might be called the source for legal enactments. But so much of law as has the sanction of truth and *its* final authority, rests not upon the state but upon the underlying realities. There are physiological laws, if we may so call them, whose authority transcends all state enact-

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ments, there are similar economic laws, and there are moral laws far more vital in human relations than any national enactments. The state is not the source of fundamental law, that which the British name "the common law." Only the enacted forms for the outworking of the principles of this body of fundamental law are dependent upon the state. Truth itself is the ultimate source of all fundamental law, and human enactments will constantly change as men reach fuller appreciation of the realities of relation that underlie human intercourse. The state is but a means for assisting the citizen to conform to the fundamental realities. The statement of the Prussian cult, that government is the source of all law and so is above all law, as President King has so well said,¹ "cannot be thought through for the government of God himself," whatever definition we may take of the concept "God." God is not the source of moral law. The source of moral law is truth itself. Truth *is*. It is not derived. It exists not because of any enactment by God or man, but in itself, and it is the ultimate source and sanction for all law.

If it be true that there is this great body of fundamental law, resting upon the realities in human character and human relations, there seems no distinction between individuals and nations in responsibility to this body of essential, self-enacted law. No man, and no group or association of men, industrial, social, political, national, or world-communal, is above such law or free in any degree from obligation to it. It seems, indeed, most strange that any group of men could ever convince themselves that they were, as a group, free from this obligation, and it seems still more strange that they could declare this freedom in so shallow a formula as the statement that "the state is the source of law and so above the law."

Among the most important of the truths of human nature and affecting human relations are those that emphasize the human capacity for well-being and the privilege of promoting human welfare, a privilege and an obligation. These truths are as real as the phenomena of mass and mass attraction between

material bodies, or any other physical natural phenomena and relations. They are an essential part of natural truth, and as such must be conformed to by any man of true scientific spirit. To disregard them is scientific dishonesty and dishonor. It is equally unscientific for an individual or for any group of individuals.

In view of these considerations can it truly be said that "the Germans are the mightiest and the greatest race and nation"? Is it not rather true that among the highly developed peoples they are somewhat unique in the degree of their failure to perceive that body of scientific truth which we commonly call moral, that in reality they are in this regard either a naturally deficient people or an undeveloped people, a people mediaeval in their character as they are in their governmental institutions?

It is peculiarly difficult to determine whether national and individual qualities are, in any instance, due to inheritance or to education. Qualities due to nurture may become, after long training, so firmly established and so highly developed as to appear natural to the stock itself. One must always walk cautiously in this field and not condemn, as inherently defective, stock that is capable of restoration by reversing the evil education.

In this connection there is one consideration, to which I have elsewhere referred,² which merits attention. "A race, a nation, makes itself; it is not made or molded chiefly by outside influences. Nations are what they have made themselves." The Germans, while always much given to philosophy, have never shown interest in moral philosophy. "Germany has never had a Carlyle, an Emerson, or a Lincoln, and this lack is no accident. John Knox, Carlyle and Lloyd-George are the product and the sign of the British fighting sense for justice. Bismarck and Goethe, with their marked lack of interest in the moral aspects of statecraft and philosophy, seem as truly characteristic of the German people." One must speak with some hesitation, for such judgments are peculiarly liable to error, but it surely seems that the somewhat unique German lack of interest in the philosophy of

morals and the moral qualities of conduct, must be due to inherent racial character.*

But whatever its source, this deficiency makes untrue the statement that "the Germans are the mightiest and the greatest race and nation." They fail to conform to those fundamental scientific realities which we commonly call moral, and this failure renders them peculiarly unadapted in an environment in which there is a gradually increasing appreciation and realization of moral relation between nations. If it be true that cooperation is increasingly to replace unrestrained rivalry between nations, and that this cooperation is to conform to the moral realities, then Germany's deficiency makes her peculiarly unfitted for the life that is to be. Lack of adaptation to environment, unfitness for life as it has to be, is not strength but weakness. It seems, therefore, that the Germans, instead of being the "mightiest and greatest race," are really quite unique in their unfitness.

In general intellectual development the Germans stand among the stronger peoples. They have had one or more preeminent and several major musicians. They had in Goethe one of the world's great poets. Kant is one of the strongest of philosophers, but his mother was Scotch. In social philosophy they have not reached beyond the ideal of economic efficiency and so have given no world-leaders. In astronomy and physics they have no rivals of Galileo, Kepler and Newton, but show a number of strong men of second rank. In zoological science they cannot equal Darwin and Pasteur, but in chemistry they show many of the ablest scholars. In invention, of course, they do not rival America, and in recent work in physics, biology and medicine Germany is hardly keeping pace with Britain and America. In general one may say German scientists have shown great diligence, much talent and some genius. In music, painting and

* Kant indeed emphasized the categorical imperative in his philosophy, but three things should be noted: 1) that Kant's philosophy was purely abstract; 2) that it has never registered in German social life, and 3) that Kant was himself half Scotch in descent and more than half Scotch in intellectual type. Luther placed his chief emphasis upon faith, and while he preached personal righteousness, it is not this part of his message that has passed into German life. His influence, as seen today, is more ecclesiastical than vital.

sculpture Germany now shows little inspiration. In the whole field of intellectual life she has had her full share of able men and has given the world a few great leaders. There is no marked intellectual lack in Germany, except her failure properly to evaluate moral phenomena, and her self-centered quality resulting in a remarkable inability to understand the psychology of other peoples.

Were there time it would be profitable to consider the historical evidence that the attempt to dominate the world by force, even when apparently successful, has not only always proven abortive after a rather brief period, but has destroyed the people who followed the false hope. Judging by the past, this hope of forcible dominance might be taken as a sign of decadence and approaching elimination. In the opinion of the writer, German triumph in the present war would be the surest and probably the shortest road to the destruction of Germany.

Any thorough discussion of German racial qualities would be appropriate to a meeting of anthropologists and ethnologists rather than zoologists, and I shall not attempt to carry it much further. We may, though, note, before leaving this phase of the subject, that the German people seem to be of mixed stock. The South German is round-headed and of moderate stature; the North German is narrow-headed and of greater stature. If the word "Teuton" is to be applied at all, it cannot well cover both of these stocks. It seems better limited to the northern type, though in this northern stock there is admixture of Slavic blood.

There seem quite clear psychic differences, as well, between the two divisions of the German people. Dickinson writes:³—"It is significant evidence of the two Germanys that not one of the great German composers was a Prussian. Bach was a Thuringian; Mozart was Bavarian; Haydn an Austrian citizen, probably a Croat; Beethoven was born in Bonn of Flemish descent, on his father's side; Weber, although born in Holstein, was an Austrian; Schubert was an Austrian; Schumann was a Saxon; Mendelssohn was a Jew, born in Hamburg; Wagner was a Saxon; Brahms was born in Hamburg, of Saxon descent."

Practically the same thing is true as to German painters, sculptors, men of letters and philosophers, and among German scientists there is great preponderance of men from South and West Germany. Indeed ex-chancellor von Bülow writes:⁴—"German intellect had already reached its zenith without the help of Prussia. German intellectual life is predominantly the work of the South and West, achieved under the protection of her princes, small states and free cities. But the people who lived in the sandy soil of the Mark, in the plains east of the Elbe and the Oder, so scantily favored by nature, during the centuries which witnessed the growth of German culture in other parts of the country, prepared the future of Germany as a state in battles and privations under the rule of heroic and politic kings. German intellect was developed in the West and South, the German state in Prussia. The princes of the West were the patrons of German culture; the Hohenzollern were the political leaders and taskmasters." And further—"Prussia this rude and thoroughly prosaic state of soldiers and officials." These quotations bear the more weight when we remember that von Bülow is himself a Prussian Junker. All who have lived in Germany know that *Gemüthlichkeit* is a southern and western quality and not Prussian. Yes, the spiritual distinctions are probably more marked than the physical differences between the Northern and Southern Germans.

If cooperation is destined to come in larger and larger measure in the world-community, and national selfishness is to give way in considerable degree to international helpfulness, then the qualities von Bülow emphasizes as most marked in the Prussian will be at a discount. Military genius will have to turn to other channels for its exercise, and state-centered statecraft must give way to a broader-visioned recognition of general human welfare. Sympathetic realization of human needs, founded upon a kindly appreciation of human character, must underlie statesmanship in the world community. It seems that so much of contribution to the larger world-life as is to be expected from Germany, is likely to come chiefly from the Southern and Western Germans. Freed from their present obsession

with the Prussian cult of abnormal exaltation of the nation, may they not perhaps return to something of the mellowness evidenced in their music, in some of their philosophy and literature, and in the childlike beauty of their folk-life? But to gain their freedom from Prussian dominance may prove a most difficult thing. They have been long trained to obedience rather than manly independence, *and they are of a stock to which such training has been possible*. There is in the Prussian Junker a true devotion to an ideal, and the inadequacy and utter unworthiness of this ideal should not blind us to the possible value of the quality of devotion. If the more human element among the Germans could be redeemed and developed and could bring Germany to more normal spiritual life, the long training in devotion to the nation might be utilized to energize the new and sounder purposes. But who can look with confidence to any such result?

Efficiency recently has been the German ideal and has been increasingly emphasized for more than a generation. But efficiency is in itself no worthy goal. It is but a means to an end. I think the world is becoming a bit weary of that efficiency which is measured in manufactured products and stored wealth. That is true efficiency which makes for human well-being. That is real efficiency which promotes not abundance of goods, but abundant life, and the chief satisfaction in life is not in comforts and ease, but in the fun of the game and the pleasure of fellowship in the playing of it.

Some of us look with a degree of hope to the time when those high and fine qualities which count in the game and its joy shall so appeal to the souls of men that marriage selection, both voluntary and under communal guidance, will gradually breed into humankind the strength and beauty that shall increasingly underlie the developing and perfecting world-community. In that day, if it comes, I think men will look back upon the German culture, or rather the Prussian cult, of the present generation, as a strange aberration.

But returning to the phenomena of the present war:—one thing seems to stand out most clearly, namely, that the moral

sense of mankind, if outraged, is a mighty factor in determining success in the struggle between nations. Germany's failure to realize this fact has cost her dear. She has failed to conform to this salient feature of her environment and must reap the result of her unfitness for life as it is in some of its most fundamental aspects. The awful demonstration of the inviolability of moral truth, as of all other truth, may prove in the end to be worth far more than even its fearful cost.

For our own nation and for all others, the lesson is emphasized that for the development of real national strength, conformity to natural law is essential, and of the categories within this great body of fundamental law that group which we call moral and spiritual is not of secondary importance. Conservation of our national resources must include promotion of moral strength and of understanding sympathy with humanity.

I will now read citations from different German writers, to show that my statement of the German position was very moderate.

First as to *German preeminence*:—

The present German emperor (1914), from a proclamation to the Army of the East: "Remember that you are the chosen people." Again from the emperor:⁵—"The greater Germany which some day must dominate all Europe."

From Professor Lasson:⁶—"We are morally and intellectually superior to other nations: we are without equals."

Die Zukunft⁷ (1901):—"After all, it is obviously the meaning of history that the white race under the leadership of the Teutons, should attain a real and definite domination of the world,"

Fritz Bley⁸ (1897):—"We are the most capable nation in every field of science, in every branch of fine arts."

Ernst Haeckel⁹:—"One single highly cultivated German warrior of those who are, alas, falling in thousands, represents a higher intellectual and moral life value than hundreds of the raw children of nature whom England and France, Russia and Italy oppose to them."

Adolf Grabowsky¹⁰ (1914):—"Today nothing is more urgent than this—that the will to conquer the world should take possession of the whole German people."

Ludwig Woltmann, "Politische Anthropologie" (1903):—"The most distinguished men in modern spiritual history were for the most part Teutons of the full blood, such as Dürer, Leonardo da Vinci, Galileo, Rembrandt, Rubens, Van Dyck, Voltaire, Kant, Wagner. Others show an intermixture of the brunette race as in the case of Dante, Raphael, Michael Angelo, Shakespeare, Luther, Goethe, Beethoven. . . . Dante, Raphael, Luther and the others were geniuses not because of, but in spite of their mixed blood. Their endowment was an inheritance from the Teutonic race. . . . The entire European civilization, even in Slav and Latin countries, is the work of the Teutonic race. . . . The Teutons are the aristocracy of humanity. . . . Whoever has the characteristics of the Teutonic race is superior. . . . The cultural value of a nation is measured by the quantity of Teutonism it contains."

Lieutenant Karl A. Kuhn¹¹ (1914):—"Kultur must build its cathedrals on hills of corpses, seas of tears, and the death-rattle of the vanquished." The mixed metaphors do not hide the thought.

Natural selection among nations

Bismarck:¹²—"Not by speeches and resolutions of majorities are the great questions of the time decided, but by iron and blood."

Nietsche:¹³—"Ye shall love peace as a means to new wars, and the short peace more than the long."

Lasson:¹⁴—"Separate states are therefore by nature in a state of war with each other. Conflict must be regarded as the essence of their relations and as the rule, friendship as accidental and exceptional."

Ernst Hasse¹⁵ (1908):—"The worst of hypocracies is the participation of Germany in the Hague conferences."

Treitschke:¹⁶—"The erection of an international court of arbitration as a permanent institution is incompatible with the nature of the state. Only in questions of second or third importance could it in any case submit itself to such a court of arbitra-

tion. . . . The living God will take care that war shall always return as a terrible medicine for the human race. . . . We have learned the moral majesty of war precisely in those of its characteristics which to superficial observers seem bestial and inhuman."

Bernhardi (1914):¹⁷—"The efforts directed toward the abolition of war must be termed not only foolish, but absolutely immoral, and must be stigmatized as unworthy of the human race. The weak nation to have the same right to live as the powerful and vigorous nation! . . . War is a biological necessity of the first importance. . . . War gives a biologically just decision."

Otfried Nippold (1913):¹⁸—" . . . war is not only from the biological and true kultural standpoint the best and noblest form of the struggle for existence, but"

Power the goal for a nation

Lasson:¹⁴—"Kultur exists for the purpose of making itself effective as power."

Treitschke:¹⁶—"The state is first of all power to assert itself. . . . Hence the obvious element of the ridiculous that attaches to the existence of small states. . . . The whole development of our company of states [the five great powers] aims unmistakably at ousting the states of second rank."

From a petition by 352 German professors in favor of annexations (1917):—"No policy of kultur without a policy of power."

Daniel Frymann (1912):¹⁹ *a propos* Belgium and Holland:—"For today only those states can assert a right to independence that can secure it sword in hand."

Germany above moral obligations

The present emperor, in a speech to the Chinese Expeditionary Force, July 27th, 1900:—"You know very well that you are to fight a cunning, brave, well armed and terrible enemy [the Boxers!]. If you come to grips with him, be assured quarter will not be given, no prisoners will be taken. Use your weapons

in such a way that for a thousand years no Chinese shall dare to look upon a German askance. Be as terrible as Attila's Huns."

Lasson:¹⁴ "In the intercourse of state with state there are no laws, and there can be none. . . . A war may be waged for political interests, but never for an idea. . . . Between states there is but one sort of right—the right of the stronger. . . . In the relations between states this right of the stronger may be said to be moral. . . . There is no legal obligation upon a state to observe treaties. . . . A state cannot commit a crime. Treaty rights are governed wholly by considerations of advantage."

Pastor Baumgarten:²⁰—"Anyone who cannot bring himself to approve from the bottom of his heart the sinking of the *Lusitania* . . . and give himself up to honest joy at this victorious exploit of German defensive power—such an one we deem no true German."

Professor Oswald Flamm (1917):²¹—"If neutrals were destroyed so that they disappeared without leaving any traces, terror would keep seamen and travellers away from the danger zones."

Otto Richard von Tannenburg²² (1911):—"A policy of sentiment is folly. Enthusiasm for humanity is idiocy. Charity should begin among one's compatriots. Politics is business. Right and wrong are notions needed in civil life only. The German people is always right, because it is the German people and because it numbers 87,000,000."

Maximilian Harden²³ (1914), one of Germany's most independent thinkers:—"Germany is striking. Who gave her leave? Her right is in her might."

Karl Peters²⁴ (1915):—"It is foolish to talk of the rights of others."

Thomas Mann²⁵ (1914):—"Kultur is above morality, reason, science."

Lieutenant Karl A. Kuhn¹¹ (1914):—"The power of the conqueror becomes the supreme moral law to which the vanquished must submit."

Clausewitz,²⁶ the great teacher of modern Germany:—In war

"the errors which proceed from a spirit of benevolence are the worst."

General von Hartmann:²⁷—"Military action in its procedure is completely ruthless. . . . Recognize no other law than that of military necessity."²⁸

Bernhardi:¹⁷—"Might is at once the supreme right."

M. Stirner:²⁹—"What does right matter to me? I have no need of it. What I can acquire by force, that I possess and enjoy. . . . I have the right to do what I have the power to do."

Rudolf Theuden (1914):³⁰—"In international relations magnanimity is wholly out of place. . . . For the will of the state no other principle exists but that of expediency, . . . selfishness, . . . farseeing, shrewdly calculating selfishness."

Also a number of quotations to show that these conceptions are not merely academic, but are put into practice.

From an official placard in Belgium:³¹—"In case any of the inhabitants fire upon soldiers of the German army, one-third of the male population will be shot."

General von Bülow;³² Belgian proclamation:—"With my authorization, the general commanding these troops has reduced the town to ashes and has had 110 persons shot."

General von der Goltz, in a proclamation in Brussels (1914):³³—"In future the inhabitants of places situated near railways and telegraph lines which have been destroyed will be punished without mercy, whether they are guilty of this destruction or not. . . . The hostages "[that have been taken in all such places]" will be shot immediately."

From the orders of the day by General Stenger, commander of the 58th Brigade, August, 28, 1914, in France:—"Beginning with today, no more prisoners are to be taken. All prisoners are to be put to death. The wounded, whether armed or not, are to be put to death. Prisoners, even when they are organized in large units, are to be put to death. No living man is to remain behind us."

Then two quotations to show that such orders were carried out

From a letter by a noncommissioned officer of the 154th Infantry, published in a Silesian paper under date of October 1914, being an account of fighting in France:³⁴—"No quarter is given. . . . The wounded are hammered and stabbed. . . . Whether they are slightly or mortally wounded, our brave musketeers save the fatherland the costly care of numerous enemies."

From a letter to his fiancée, by a Bavarian soldier, Johan Wenger (1915):³⁵—"I have also bayoneted a good number of women. During the battle of Budonwiller, I did away with four women and seven young girls in five minutes. The captain told me to shoot these French sows, but I preferred to run my bayonet through them." Whether this soldier did as described, or was only boasting of a noble deed to which he could not honestly lay claim, makes little difference in its bearing upon the point under consideration.

I feel I almost should apologize for reading to you such citations, those from the emperor and all through the list, but the facts must be faced.

Finally in regard to racial qualities

A single quotation from the poet Goethe:—"The Prussians are cruel by nature; civilization will make them ferocious."

The Orchard Laboratory,
Oberlin, Ohio,
December 10, 1917

CITATIONS

¹ Henry C. King: "Grounds of Hope in the Changing world Order," 1917.

² Maynard M. Metcalf: "The Problem of Germany," New York Times, Sunday, September 16, 1917.

³ Edward Dickinson, quoted by John Burroughs: "A Dual Germany," New York Times, April 19, 1917.

⁴ "Imperial Germany."

⁵ From a proclamation of June 5, 1915.

⁶ From a letter published in "The Amsterdammer," October 11, 1914.

⁷ September 7, 1901.

⁸ "Die Weltstellung des Deutschen."

- ⁹ "Ewigkeit: Weltkriegsgedanken," 1915.
- ¹⁰ "Das Neue Deutschland."
- ¹¹ "Die Wahren Ursachen des Weltkrieges."
- ¹² Addressed to the military committee of the Prussian Chamber of Deputies, 1862.
- ¹³ "Thus Spake Zarathustra," translated by Common, 1911.
- ¹⁴ "Das Kultur und der Krieg."
- ¹⁵ "Die Zukunft des deutschen Volkstums," 1918.
- ¹⁶ "Politik."
- ¹⁷ "Germany and the Next War," translated by Powles, 1912.
- ¹⁸ "Der deutsche Chauvinismus."
- ¹⁹ "Wenn ich der Kaiser Wär," 1912.
- ²⁰ "Deutsche Reden in schwerer Zeit," No. 25.
- ²¹ Die Woche, quoted in New York Times, May 15, 1917.
- ²² "Grossdeutschland: Die Aufgabe des zwanzigsten Jahrhunderts."
- ²³ Die Zukunft.
- ²⁴ "Not und Weg."
- ²⁵ Neue Rundschau, November, 1914.
- ²⁶ "On War."
- ²⁷ "Militärische Notwendigkeit und Humanität, in "Deutsche Rundschau," xiii, 1877.
- ²⁸ Idem, xiv, 1878.
- ²⁹ "Der Einzige und sein Eigentum."
- ³⁰ "Was uns der Krieg bringen muss," 1914.
- ³¹ Hasselt, Belgium, August 17, 1914.
- ³² Liege, Belgium, August 22, 1914.
- ³³ Brussels, Belgium October 5, 1914.
- ³⁴ Jauersches Tageblatt, October 18, 1914.
- ³⁵ Dated Peronne, March 16, 1915.

SYMPOSIUM

THE TEACHING OF ANATOMY AND THE INCULCA- TION OF SCIENTIFIC METHODS AND INTEREST

*Given during the thirty-fourth session of the American Association
of Anatomists, University of Minnesota, December 27, 1917*

THE VALUE OF THE ROENTGEN-RAY AND THE LIVING MODEL IN TEACHING AND RESEARCH IN HUMAN ANATOMY

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The practical value of roentgenology in clinical work has led to extensive studies of the structure of the body as revealed by variations in tissue density. New light has been thrown on the anatomy not only of the skeletal system, but also of other parts of the body especially of the thoracic and abdominal viscera. In the main, these studies have been made by clinicians who have had no highly trained technical knowledge of anatomy and no special facilities for comparing the anatomy of the living as revealed by variations in tissue density with the anatomy of the dead as revealed by technical preparation. On the other hand, few anatomists have made themselves familiar with the data revealed by the x-ray studies of clinicians or with the possibilities of correlating the anatomy of the dead with the anatomy of the living revealed by the x-rays. Roentgenology offers an attractive field for research to the anatomist and a fertile field for vivifying his work as a teacher.

Of the various subjects of the medical curriculum, anatomy offers the best opportunity for training the student in habits of resourceful independence. The student can be allowed to wander

from a straight and narrow path and to make mistakes until he acquires self-mastery, because the resulting loss is that of a little time and material. In the chemical laboratory, if allowed too much freedom, he may blow up himself and his fellows. In the physiological laboratory or the clinic he may cause too much needless suffering. In the dissecting-room a student may wisely be allowed considerable freedom when held up strictly for results. The most important thing he can get from the dissecting-room is the habit of independent workmanship with constant aim at results that show skill.

When students are given this sort of training in human anatomy, for which we are largely indebted to the genius of the late Franklin P. Mall, they gain self-mastery, which carries them far in their subsequent medical careers. But while they may acquire considerable manual dexterity and considerable skill in observation, they are apt to neglect the imaginative reflection which is necessary for translating observation into work of value. As a means of stimulating the imagination in gross human anatomy roentgenograms are of considerable value, especially when study of the roentgenograms is combined with fluoroscopic studies on the living. The use of the roentgenograms belongs in the realm of work in which students may be given a free hand, since the worst that can happen is injury to a few plates. The taking of the roentgenograms and the use of x-ray machines for fluoroscopy, on the other hand, has to be carried on under strict supervision and therefore is of little value as a general means of training in independent initiative, although of good value in adding interest to the study of anatomy.

At the University of Wisconsin we have made a beginning in the systematic use of roentgenology in connection with anatomical study, but I feel that a far more extensive use might be made with advantage.

For the benefit of our first-year students who are beginning the study of human anatomy we have a set of x-ray plates displayed in a room conveniently situated near the dissecting-rooms, and the students are encouraged to study these plates in connection with their work in dissecting. So far as possible pairs of stereo-

scopic plates are used and prismatic stereoscopes are provided for the study of these plates. The skeleton is well illustrated with especial reference to the joints in various positions and to the air sinuses of the skull. Plates are provided to display the anatomy of the heart and of the lungs. The abdominal viscera are shown both with and without the preceding ingestion of barium meals. Most of the plates are made from the living, both children and adults, but some roentgenograms are provided of specimens especially injected after death to show blood-vessels and other features. I believe that this latter feature could wisely be extended. Our plates along these lines have come chiefly from the research work of Dr. Miller and Dr. Dunham on the lungs.

On the whole, I have thus far been somewhat disappointed at the lack of free independent use of the plates by the majority of the students. They readily go into the room with an instructor and express great interest in what he points out, but comparatively few students study the plates carefully on their own initiative. The same men later in private practice will study x-ray plates carefully in connection with suspected fracture cases because here the study is a means to a definite end. It is hard to make the student feel the same interest in plates that might help him to understand better the part he is dissecting. It is probable that a better arrangement of plates and more careful labeling than we have provided would help. The students can be made to study the plates by requesting outline drawings with parts labeled.

During the second semester of the first-year students are taken in small groups to the fluoroscopic room of the x-ray department of the medical school and are shown the action of the various joints, the expansion and contraction of the thoracic cavity, the beating of the heart, the ingestion of a barium meal, and other physiological activities of the body, the different members of the group taking turn as subjects. The students always show more interest in fluoroscopy of the living than in roentgenograms. If it could only safely be done, a great deal of interest might be added to the study of anatomy by turning over an x-ray transformer and a fluoroscopic outfit freely for the use of the students during the study of anatomy. But the danger of x-ray burns

precludes this. The supervised and therefore limited use of fluoroscopy in teaching anatomy can wisely be combined with the study of structure in action as revealed by visual observation, palpation, and precussion of the nude living model. We have endeavored to do this by the employment of students as models for certain hours each week during the second semester of the first year, and I believe with profit. Artists' models trained for this special work would probably be better than the untrained models we make use of.

For many of the advanced students in human anatomy roentgenology has proved even more stimulating than for the beginning students. We make it a regular part of our work in topographical anatomy somewhat along the lines described above for beginning students but more extended. Seniors in the College of Letters and Science and graduate students who are candidates for a Master's degree, while carrying on medical studies, are required to present a thesis. When this thesis is chosen in topographical anatomy the student is usually assigned to some topic in which the recent work in the field of roentgenology has added something to our knowledge and is encouraged to try to add something of his own. These students have all shown great interest in this work. Several papers embodying the results are now in course of revision for publication. Advanced students of this character can, of course, be given more latitude in the use of x-ray apparatus than can be given to beginners.

The ready willingness of students in the dissecting-room to aid members of the staff and advanced students by making special dissections which help to unravel the mysteries of light and shade in roentgenograms contributes to scientific research, to the interest in teaching, and to the interest in study.

2. WAYS AND MEANS IN THE TEACHING OF GROSS ANATOMY

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There are certain objections to the course in gross anatomy made by the average medical student which must be taken into consideration in a discussion of the pedagogy of the subject. It is not my purpose to advise the adjustment of any course so that it will meet with the approval of the student, and in particular, with the medical student. It may be said that medical students have been so often exposed to or vaccinated by the various science courses in the required premedical curriculum that they appear to be relatively immune to the intrusion of new ideas, either as to subject matter or methods of presentation. This immunity to learning is rendered the more effective by the gratuitous advice of the successful practitioner, whose memory of the actual work of his student days is somewhat hazy, just as the quality of this said work has been somewhat enhanced in the telling, and by a halo of age. In defense, however, of our colleague, the practitioner, it must be noted that he uniformly advises the prospective medical student to 'know his anatomy.' I have made repeated efforts to run down exactly what this valuable suggestion may mean, but without success. The result is that the medical student comes to the dissecting-room with an interest which is not paralleled in any other subject of the elementary medical curriculum. In addition, the student has a certain amount of preparation in vertebrate anatomy—more or less misbegotten because he has regarded the study of vertebrate zoology as one of the necessary evils of the premedic years. There are three of these evils like the 'Three Musketeers of Dumas; physics, chemistry, language, and biology; named, as nearly as I can figure them, in bigbear order. It follows, therefore, that our novice in the course in gross anatomy

comes to us nowadays with the interest he possessed some twenty years ago, with certain more or less fundamental conceptions regarding vertebrate structure, and possibly with ideas concerning the phylogenetic relations of the more important organs. He naturally expects from a hurried dissection of the chief vertebrate forms that he is preparing to understand the relations in the human body the better. If his instructor does not materialize a comparative explanation or does not pitch the work on a plane which presupposes information the student has gleaned from actual contact with lower forms, the student is likely to ask himself an embarrassing question, "Why is vertebrate zoology a requirement for the study of gross anatomy?" He may also find a ready answer to the question by passing the word down the line "Get through somehow. You won't use it, anyway." If our premedical requirement is merely to furnish us with students two years older, and who have supplemented all of the bad habits of study in the high school with many of the vicious mental tricks of the college student, I, for one, would feel that the requirement has undergone a perversion in function.

All of us who have enjoyed a varied experience realize that all students may be divided into three classes: Those who are genuinely interested in the work and who take advantage of all of the opportunities because they really like the thing they do; those who are interested because the subject is made interesting to them, and, finally, the spoon-fed, led-by-the-hand variety who must have the subject 'learned' to them and whose main ambition in any subject is to outguess the instructor on examination questions and get by with it. The first-named variety comprises the very desirable class of students who learn in spite of their teachers; the second learn because of their teachers, and the third and unfortunately large per cent should contribute to a mortality list even more than they do. Yet even with them we must temper justice with mercy because they are a result of a mind-improving educational system which places a premium on learning the thing for the thing itself. Given a student whose mind has been so thoroughly cultivated that he cannot see the woods for the trees, and you have a desperate pedagogic problem. Add to this the lack

of initiative which usually accompanies this serious condition, and you have the pest who follows one about the laboratory absorbing ideas like a sponge sops up laboratory stains, and giving out these ideas under pressure with somewhat similarly mixed results.

It was my doubtful privilege, and one which I am sure the majority of you have not enjoyed, to put in my first course in anatomy under the old system. Gray's Anatomy was the family bible, and I gained a horror of systematic text-book recitation which has always stayed with me. The book was the thing and the body was merely an accessory after the fact, mutilated at night under the most sordid of conditions. It was at this time that the three-year medical course changed to four, and a laboratory method of teaching anatomy began largely, as I recall it, through the efforts of the late Professor Mall. Then the pendulum swung to the other extreme. No longer did the surgeon hold opera-glass clinics on a dissected cadaver. No longer was the dissecting-room work a sort of black art. In place of this, lectures became conspicuous in their absence and dissection became a day-light laboratory subject, and professional anatomists began to move in polite society. The swing to the research worker was a direct protest of those who knew, that anatomy was being poorly taught, and I will hark back to this later.

If I were to translate myself back some twenty years ago what were my thoughts and criticisms of the course in gross anatomy. I resented being kicked out of the dissecting-room after forty-eight hours' dissection of the lower half of the body, and registered my resentment by putting in several weeks the following summer with Professor Kerr in working out the relations of superficial to deep lymphatics of the axilla. The most successful as well as the most spinal piece of dissecting I accuse myself of. Successful in that Gray and I differed. I worked through the osteology with a skeleton nearby and wondered why it was so essential to know all of the wrinkles and dimples and foramina with which various bones were excruciatingly and inaccessibly beset. I went over a collection of joints and wondered what kind of eye the man had who drew those delightfully crisp ligament separations. I protested the systematic origin, insertion, innervation, and rela-

tions of the individual muscles and maintained it couldn't be done, especially when we tripped up our instructor at times. I recall memorizing anastomoses between various arteries because it seemed to me they were at one time considered important and therefore wished on to future generations. I figured the veins were easily as important and far more complicated than the arteries and why so little devoted to them in the text. The various plexuses of nerves were as nightmares, and so thoroughly did I bone their form that I could draw them upside down and backwards to prove that I really knew something of them. The brain was a chamber of nomenclature horrors, and I shone in my fraternity as the individual who had actually dissected a brain and was held, next to Gray, as the last word on the subject. Please remember I came into this work younger than most students and therefore more pliable; brought up in a museum, which may account for some of my peculiarities, then and now, but extremely eager to work and learn.

This, then, leads us to the second point I would make. One does not expect a student to swallow, digest, and assimilate all of the data of gross anatomy, and therefore some of the matter must be filtered out as more important as opposed to certain matter which must logically be less important. Essentials of anatomy do not exist. All of them are de-horned species of text-books with fewer adjectives, verbs, and prepositions. Condensation does not make for digestibility any more than bulk makes the matter more easily assimilated, and because of this we have a teacher. I take the liberty of contrasting the teacher with the research worker. Both of these individuals are a result of brains and application. Neither of them are born. Both represent men whose receptive apparatus and analytical power is or should be better developed than their motor discharge. There are, however, two requirements in the teacher which need not be found in the research worker. The first of these is a personal interest in students, and the second, an interesting personality to his students. Personal interest in students is not synonymous with research worker, and the interesting personality may make itself known in a vicarious inspiration which the student is supposed to obtain through fleeting

glimpses of a great man comparing the rotation of the extremity joints of the grasshopper with similar appendages in the cousin cricket, or what you will. Therefore, we must teach our students well because we are interested in the teaching, or not at all because we are not interested; either method is excellent and between the two lies mediocrity. If we are to select for our positions as teachers of gross anatomy those individuals whose greatest merit lies in the bulk of productive work or in the seduction of students to do a great amount of this work for them, we must not expect any marked increase in the efficiency of our teaching.

The teacher of gross anatomy of limited experience, say only five years, certainly must have developed some idea of what is more important and what is less important. The learning of the subject for itself has been abandoned together with other mind-improving ilk. Facts in themselves do not constitute knowledge. They are merely the letters which spell knowledge, information, or what you will. It is the privilege of an individual possessed of a functional cortex to limit memory largely to subconscious or sub-cortical functions. It is the privilege of the intelligent man to forget things, and the more intellectual he is the more he makes it a point to keep his mind free. It is only the idiot who cannot help remembering. We make it our business nowadays, I believe, to teach things that they may be forgotten, and if any of you are in doubt whether this is your method or not I will give you a simple formula. If, when you lecture or quiz your students, you translate your own personality and wonder what it would all sound like if you were on the benches and what you would remember of it all the next day, I maintain you belong to the desirable class. I do not anticipate approval of this method of approaching students. It would be undesirable if there was an approved method because it would show a lack of individuality in teachers which is one of the prime requirements. If, however, you feed the mental pabulum without any regard to the student's powers of assimilation; if you follow your notes year in and year out because it is the easiest way; if you cannot make your teaching the personal matter with all of its personal equation; if you concentrate your courses in your own interests rather than in those of your students: I, for

one, as a representative medical student would get little information or inspiration from your work. I hark back, therefore, to the transition of anatomy as a didactic subject to one of purely laboratory experience and refer to the pendulum coming to a more midway position. Because we have professional anatomists nowadays; because we have men of experience; because we have research workers—although prominent men in gross anatomical research are relatively infrequent; therefore we give our students opportunity to profit by experience and learn through their ears as well as their eyes. The advantage of ear learning over eye is obvious. One can't strain one's ears.

Personally, I believe that if an instructor demands more, or as much, of his students than he himself can deliver after years of experience, of observation and review; after viewing hundreds of dissections to the student's one, this individual in my opinion does not have a fundamental conception of the subject and his students will get farther through his neglect rather than his interference. How successful is each one of us as a teacher? How often do we take inventory as to exactly how good we are at it? One cannot measure the efficiency of one's teaching ability by a criterion of examination any more than one can gauge the productiveness of his research with a bibliographic calipers. It is the blissful privilege of the true teacher to be discouraged, and because of his discouragement to ever try anew. If, therefore, you are perfectly satisfied with your method of teaching or perfectly contented with the results of your research, it means you are slipping or have slipped. Personally, I teach anatomy because a student will forget it, and do not let us make the common mistake of confusing the forgetting of a thing with the never-having-known the thing.

I have thus far tried to tell something of the medical student and his resistance and his conferred or acquired immunity. I have also attempted in an impersonal sort of way to tell who is the teacher of gross anatomy. I shall next unscrew the inscrutable and tell you what we should teach, and finally camouflage the impossible by telling you how to do it. I reserve the right to deal negatively with the problem if I so choose in the interests of brevity and universal peace.

What shall we teach our students in gross anatomy? It is difficult indeed to make categorical statements on what one must do and what one must not do. Perhaps our discussion of the pedagogy of a subject would not suffer if the essayists were less theoretical and more practical. There has always been a suspicion in so-called standardized courses that the standardization consists in "not doing as I do, but doing as I tell you." Perhaps it may be a good idea and the easiest way out of the difficulty to make it a personal quantity even if the method shines negatively in contrast with your own excellent views on the problem. In the teaching of gross anatomy I attempt to do five things: I encourage dexterity in dissection; a purposeful dissection; an independence in observation; a justification of facts, and, finally, a weaving together of some sort of plot to the story of the body.

The training of a digital dexterity is a valuable asset to the medical student and it is a good thing to emphasize that it represents a sort of spinal busy work, but much good comes of it in a profession where a man is supposed to use his hands as well as his brains. Please do not misunderstand that I hold excellent dissection as equivalent to good anatomical work. We have all had students who dissect beautifully and know little of what they do and, conversely, students who dissect very poorly, but know a great deal about it. The tendency on the part of the average student is to be in too great a hurry, and I do not encourage anyone to save time any more than I stimulate them to improve their minds. It is also a bad plan to install into the heart of students that the cutting of this or the tearing of that is such a terrible offense. The only way I know to tell how much traction a nerve will stand is to pull a few of them in two. There is a very arbitrary line between poor dissection and mutilation of the dead and the essential difference is like that between falsehood and lying—the intention.

Students are supposed to be dissecting, inasmuch as the work is largely spinal, to some purpose, and this purpose, I take it, is to check on the structures as they find them in the text. The body after all is the thing and the text is merely accessory after the fact. It not infrequently happens that students see structures very

well as evidenced from the dissection (superior colliculus), and they also at the same time see things very poorly as far as the lateral geniculates are concerned. A purposeful dissection demands more than merely doing a good dissection and checking the structures found in the book. It demands an independence of observation; an interest in similar structures on the other side of the body or in other bodies.

Too much guidance—too many directions are probably worse than none at all, because the student is supposed to have some initiative. It is a good plan, I find, not to go into great detail, but let the student work it out for himself as much as possible. It is also an excellent idea to sit down with the student once in a while and show him you can do the work yourself as well as talk about it. The best way to encourage observation in a student is to observe with him and not at him or to him.

If you tell a man the earth is not an oblate spheroid, but a truncated tetrahedron, it is merely a waste of words unless he reacts and wonders why. Justification of facts to me means this: first, it leads to an understanding of the relation of structure to function; second, the information is essential to a comprehension of abnormal structure and function; third, it is of interest from a phylogenetic standpoint to one who should be a student of evolution; fourth, it bears on the fundamentals governing the developmental processes, and, lastly, certain data are important to the proper conception of cross-section anatomy.

There is no justification for the absolute divorce between anatomy and physiology or anatomy and pathology, and it may be the anatomist is not as good a general physiologist and pathologist as the latter two are anatomists. The instructor certainly cannot expect a student with less time, interest, and experience to weave a pattern out of a mass of facts when the instructor himself cannot do it. I, for one, am anxious to hear Professor Jackson's paper and Professor Huntington's paper, which ought to let no little light in on the problem, provided they tell us how and what they do. It is safe to say that details must go, and whether this artery has fourteen named branches and yonder twenty-two is of little consequence if one does not know the general territory involved. It is a good thing to know that the internal carotid has most of its

distribution inside the skull and that the external carotid is mostly outside the skull. It is folly to make the student memorize the origin, insertion, innervation, and action of muscles because the physiologist proves to him that all a muscle can do is shorten and that no muscle contracts by itself—in fact, leads him into reciprocal innervations for an answer. So the militant student comes to us for a justification, and either we hand him the worn-out adage, “Learn the thing for the thing itself,” or we explain why it is important, or we agree with him. Personally, I agree with him. The most important thing about a muscle is the position of its tendon to the plane of action in a joint. The same holds true of the details of anastomosis except from an historical interest, and the peripheral communication of nerves which, according to the physiologist, do not communicate.

Whatever may have been the sins of the academic courses, let us make what we teach to our students of a kind that will make them more receptive to later study of subjects which comprise their life work; at least let us not contribute to their resistance.

How you shall teach gross anatomy is quite inseparable from what you teach, and therefore depends both on teacher and teachee. I have said that the teacher must have an interesting personality and must be interested in the welfare of his students. The student must be receptive, and in order that he be receptive, he will expect action on the part of the teacher; accessibility of information; interpretation of importance from the teacher's standpoint, and, finally, interest and inspiration. Interpreted the other way around, the teacher must translate himself into the person of his students. The student is usually loyal and will apologize for a poor teacher by saying “there is little question but that he knows his subject.” If, therefore, we, as teachers, maintain the right to analyze how much our students know by their motor discharge, it is only fair that the student apply the same rule because a good teacher is at the same time one of his own pupils.

Next to remoteness in the person of the instructor comes inaccessibility of information. Just as I stated, too much guidance in dissection develops mental lean-to's in the students just so too much stereopticon, too much microprojection, too many

charts and museum specimens contribute to making information inaccessible to the student because we tend to make what constitutes a perfectly obvious thing remote. It has been said that the college course in physics is greatly interfered with through the chicanery of appliances and apparatus. It is just like telling a story to illustrate a point. If the story is too well told the student will remember the story and forget what it was intended to explain. It is my opinion, therefore, that the more offhand the information, the more schematic the idea, the less like the original, the better it will take; bearing in mind justification must underlie all information, imparted or required.

The next point I made was in reference to interpretation of the importance of certain facts which does not mean spinning out in an hour's lecture what a student may read somewhere in fifteen minutes. It consists in the teacher's telling the results of his own observation from his own experience and is therefore mainly matter which is not to be found in a text-book. This is a problem which requires a great amount of time and study, and this is the sort of thing that does more to inspire the student than any one other thing I know. Lectures of this kind require experience, confidence and a certain amount of philosophy, and are either to be classed as valuable adjuncts to teaching or very bad. It is much better to convince the students by precept, by word of mouth, and by action that no subject of vital interest can be difficult to a man who has the brains, the application, the facilities, and the incentive to work, but without the incentive the results are ineffective.

The advice given in a symposium like this will not materially affect us—the older men whose mental and physical habits are well formed—too well formed perhaps to allow even a moderate elasticity. Rather this recital of admonitions and experiences will do much to steer the younger men toward a more friendly personal interest in their respective flocks and perhaps for the same reason that they do their research work—because they like to do it. There is a great future ahead in this country for the man who will take the teaching of gross anatomy seriously, and will take it seriously because he likes it.

3. HOW CAN ANATOMY BE TAUGHT AS A SCIENCE AND FULFILL ITS PURPOSE AS A FOUNDATION FOR MEDICINE?

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It is now generally agreed that in medical schools the fundamental branches should be taught primarily as sciences, but at the same time with a view to their purpose as a foundation for medicine. Thus anatomy on the one hand must furnish a comprehensive and rational explanation of the form and structure of the human body, and on the other hand it must provide a 'working knowledge' as a basis for subsequent study in physiology, pathology, and clinical medicine. This ideal with its twofold purpose is clear. The question is, can it be realized? And, if so, how is it to be done?

The primary purpose—to teach human anatomy as a science—is, at least in theory, not an especially difficult problem. In general, the object is to study the human mechanism in the light of its individual and racial history; to explain the human body as a biological organism. Given a competent teacher, students familiar with the principles of animal morphology, and the facilities of a modern anatomical laboratory, this task could readily be accomplished. It would require merely a carefully planned lecture and laboratory course, including a brief dissection of the human body, with correlated work in histology and embryology.

But this knowledge of the general principles of human morphology, while indispensable, is insufficient for the needs of the medical student. His training must include more. He needs in addition many specific details of human structure which are necessary to solve the problems of physiology, pathology, and

clinical medicine. To teach anatomy as a science and at the same time to meet the requirement for specific knowledge in the brief time available is the difficult task which confronts us as teachers of anatomy.

From the clinical point of view, it is desirable that the medical student should know all about human anatomy, since the exact details needed cannot be foreseen. Yet this is clearly impossible. The student might easily spend years in the study of gross anatomy alone, without exhausting the subject.

It is evident that there must be a selection of the subject matter to be taught. The best that can be done is in teaching anatomy as a science to use as illustrative material so far as possible those concrete details most likely to be of use later and to present them in such a way as to give the student a collateral training which will be of maximum value.

To make wisely this selection of subject matter with a view to its practical application later requires of the anatomist a knowledge of the subsequent work in medicine. While it is not necessary for him to be a graduate in medicine, he should at least have a sufficient comprehension of physiology, pathology, and clinical medicine to judge as to what will probably constitute the most useful preparation for these subjects.

Even with the best possible selection of subject material, much anatomy which the student may need must necessarily be omitted. The situation is materially improved, however, if the elective principle is adopted in the medical curriculum. According to this principle, it is frankly recognized that no student can be expected to learn all about every useful subject in the curriculum. He can hope at best merely to get a fair grasp of the fundamental principles in each subject, with such details and training in handling them as will serve his purpose in the more frequently met and important phases of medical science and practice.

By cutting down the various required courses to the bare essentials, the medical curriculum, now overcrowded in most schools, can be somewhat reduced so as to give room for electives. This will permit the individual student to supplement his required courses by further elective work in the lines of his greatest needs,

and thus give him a training better than is possible with an inflexible curriculum. While the time which can thus be devoted to electives is necessarily limited, the system is a decided improvement. Although but few medical schools have as yet adopted this principle, many more will doubtless do so when its advantages are better understood.

Our experience with the elective system in the Medical School of the University of Minnesota may be of interest in this connection. In 1914 we reduced our overcrowded and inflexible medical curriculum from a total of about 4,800 hours to 3,624 hours of required work. Throughout the sophomore, junior, and senior years, on two half-days a week no required work is now scheduled, this time being left open for elective courses offered in the various departments. From these elective courses, each student must choose the equivalent of six hours a week, or a total of 576 hours in the three years. Thus about 14 per cent of the curriculum is made up of electives, which may be chosen in any line for which the student is prepared.

In general, the system has worked out well, and is very satisfactory to both students and faculty. As in other departments, the amount of required work in anatomy had to be reduced, in order to give room for electives in the curriculum. By abbreviating some of the courses, and making topographic anatomy elective, the required work in the department of anatomy (including gross anatomy, histology, and embryology) was reduced from 832 hours to 688 hours. This required work is now distributed as follows:

SUBJECT	HOURS	YEAR
Gross anatomy.....	336	First
Histology.....	160	First
Embryology.....	96	First
Neurology.....	96	Second
Total.....	688	

Various electives are offered in the department of anatomy, with enrollment during the past year as follows:

Special dissections.....	32
Topographic anatomy.....	14
Applied anatomy.....	14
Advanced anatomy.....	18
Anatomical drawings.....	3
Anatomical technique.....	13
Advanced histology.....	23
Implantation and placentation.....	3
Fetal anatomy.....	13
Special embryology.....	8
Experimental neurology.....	5
Research in anatomy.....	10
Anatomical seminar.....	8
Total enrollment.....	164

These electives vary in time, the average occupying about 80 hours. Thus, the total of the electives taken in anatomy amounts to an average of nearly 170 hours for each student in a class of 75. This would bring the total average per student up to about 858 hours (required and elective), or slightly more than that formerly required of every student. Even though the total amount of time devoted to anatomy were the same, the efficiency of the instruction would be increased, because the work is distributed more in accordance with the varying needs and capabilities of the individual student.

The elective system requires more work by the staff, for it is evident that to teach several shorter, more specialized courses to students in small groups will require more work than to teach an equivalent amount of routine class work to students in larger groups. But the results justify the increased work by the staff, and the elective courses are profitable to the teachers themselves as well as to the students.

The students who choose their elective work in anatomy do so for various reasons. A few (would there were more!) take advanced anatomy because they become interested in the subject for its own sake or as a possible career. The majority elect it because they realize the advantage of a more extensive training in

anatomy as a foundation for clinical work. Some have in mind a better preparation for definite clinical fields in which they hope later to specialize. Whatever their purpose, the elective system permits them to obtain a training in anatomy far better than would be possible under the inflexible required system.

Another phase of increasing importance in medical education which concerns anatomy is the graduate work. The modern university must meet the growing demand for trained specialists in the various fields. In this connection, anatomy is concerned, 1) in the training of anatomists themselves, as recruits to the profession and, 2) in contributing to the training of specialists in other fields. As a major line of graduate work, anatomy should be open to candidates for the Master's or Doctor's (Ph.D.) degree in the graduate school on the same basis as any other scientific subject. Teaching fellowships should be provided which will help to defray the student's expenses, while the experience in teaching will probably be of great value to him in his future career. The training of recruits for the profession of anatomical teaching and research is an important phase of our work which deserves careful consideration.

The most recent phase of graduate medical education is in the clinical branches. Even under the elective system it is a recognized impossibility to provide adequate training for specialists in the various departments of medicine and surgery in the undergraduate curriculum. For the adequate training of such specialists, at least three years of graduate work are now generally considered essential, and the universities are beginning to make definite provision for the establishment of such courses. In this new field of graduate medical education, anatomy is also directly concerned, as is evident when the requirements for adequate training in clinical subjects are considered.

In graduate clinical work, as in graduate work generally, no definite and fixed curriculum can be formulated, the work being advanced in character and adapted to the individual student. Certain general principles are self-evident, however, and should be kept clearly in mind in planning the work in each case. It must be remembered that in anatomy, as in the other funda-

mental sciences, the training of the average medical student (as we have seen) has necessarily been limited to that which may suffice for purposes of general practice. If he desires to specialize in any clinical branch, he must strengthen his foundation by further work in the fundamentals, otherwise the clinical superstructure will be unsatisfactory. Just as anatomy, physiology, and pathology form the foundation upon which the undergraduate clinical training is supported, so must more extensive work in these fundamentals form the basis for any efficient system of graduate training in specialized clinical lines.

We have had considerable experience at Minnesota during the past few years in the development of graduate work in the clinical subjects, and it may be of interest to know how it works out with reference to anatomy. As might be expected, those specializing in the various phases of internal medicine require, as a rule, comparatively little additional work in anatomy. In surgery and allied subjects, however, the graduate students find it profitable to spend a considerable amount of time on advanced work in anatomy. They frequently make anatomy their minor department in working for advanced clinical degrees.

In ophthalmology and oto-laryngology, for example, the graduate students usually take advanced work in anatomy for two half-days a week during the first year. In the first semester this work is in gross anatomy, consisting of 1) a review of the skull, with intensive study of special preparations; 2) topographic anatomy of the head and neck, studied especially by sections in the three planes, and, 3) special dissections for the regional anatomy of the eye, ear, nose, and throat. This is followed in the second semester by a similar study of the special histology and embryology of the eye, ear, nose, and throat, including gross fetal dissections and histological preparations of these regions in the human embryo and adult. Those making anatomy a minor are required to take additional work in some appropriate phase of the subject. For example, the wax-cast model of the adult nasal cavity and paranasal sinuses (which is demonstrated at this meeting) was constructed by Dr. Connor as a part of his work for a minor in anatomy.

Thus it is evident that anatomy must play a rôle of increasing importance in the development of graduate work, not only in the training of professional anatomists, but also in the training of clinical specialists in the various branches. In these new fields of anatomical work, as well as in the older and more familiar lines, the question of methods of teaching is one of perennial interest. Lack of time prohibits me from considering pedagogical methods, aside from a few general principles which may be briefly mentioned.

In the first place, uniformity of methods in teaching anatomy is unnecessary and even undesirable. The methods would naturally vary according to the preparation and ability of the students, the facilities available, and the individuality of the teacher. To be efficient, however, they should regard the past, the present, and the future. As to the past, the instruction in anatomy should of course be closely related to the previous work in zoology. As to the present, every effort should be made to correlate the work in gross anatomy with that in histology and embryology. And the future applications should be kept constantly in mind, as has already been emphasized.

The physiological view-point is one which is often very useful in teaching anatomy, even though we may not go so far as to admit that "anatomy without physiology is like an old maid without a dowry." In reviewing the locomotor apparatus, for example, I have found it a stimulating exercise for the students to reason out what symptoms would be expected if a given nerve trunk were cut and to give a complete explanation of the various structures involved. In the case of a mixed nerve, such as the femoral, this would involve both sensory and motor symptoms. The explanation of the sensory symptoms would include the distribution of the various sensory branches to corresponding areas of partial or complete anesthesia in the integument, joints, and muscles. The explanation of the motor symptoms would include, in the first place, the posture of the part, due to the unopposed action of the unparalyzed muscles. In the second place, it would include the movements which would be weakened or lost, due to partial or complete paralysis of the muscle groups innervated by

the various branches of the nerve. Such an explanation thus involves a review of the anatomy of the nerves, muscles, bones, and joints in considerable detail. But it does more in that it helps to organize that knowledge into a workable form of obvious value later not only for physiology, but also for clinical medicine. In general, in our methods of teaching we should always bear in mind that, as ex-President Eliot has said, professional training is primarily not for information, but for power.

To summarize briefly: human anatomy can be taught as a science, and must be if it is to be efficient. By a judicious choice of methods and selection of subject matter, it can also fulfill its purpose as a foundation for medicine. The difficulties due to the limitation of time may be largely overcome by the adoption in the medical curriculum of the elective principle, permitting students to take supplementary work in anatomy corresponding to their individual needs. Graduate courses in anatomy should also be provided for those desiring to specialize further, either in anatomy or in other medical subjects. The methods of instruction in anatomy may vary, but they should always have due regard for the preparation of the student, should correlate closely the various phases of the work, and should develop a 'working knowledge' which will serve as a basis for future application.

4. MODERN PROBLEMS OF EVOLUTION, VARIATION AND INHERITANCE IN THE ANATOMICAL PART OF THE MEDICAL CURRICULUM

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The questions assigned to this part of our discussion are becoming increasingly important from the standpoint both of general education and of the special training in medicine. To a large degree they and cognate topics are already recognized as necessary parts of a liberal education, and as such are incorporated in undergraduate teaching. Their particular significance in the field of the medical sciences and study has led to important and far-reaching changes in pedagogic methods. It would be difficult to overestimate the value of the biological pre-medical courses offered by our leading institutions in their departments of zoology, embryology, histology and comparative anatomy. They afford an indispensable framework upon which the detailed consideration of the problems here under discussion can be based in their important and intimate relations to the study of Medicine. It is necessary that the modern medical curriculum should fully recognize the obligation placed upon it by the progress of scientific thought and method, and make formal provision for meeting the same.

The anatomical course is preeminently the proper place in which this teaching should be developed, because the material facts upon which it is based, and which furnish the necessary background of illustration and demonstration, fall to a large extent already within the province of Anatomy, and require relatively slight expenditure of teaching time and effort in order to develop their bearing on the broader themes indicated in this section of our Symposium.

In modern anatomical teaching the historic distinction between

“gross” and “minute” anatomy has effaced itself completely, and the structure of the adult human body is considered as a whole from the three standpoints of its development, its resulting form and its relation to general vertebrate organization. Embryology and Comparative Anatomy thus necessarily become the guiding lines employed concurrently by the student in the acquisition of his anatomical knowledge. It then becomes merely a question at what points in the course, and to what extent, the teacher, in following these already existing lines, will direct the student's attention to the problems here under discussion.

The following gives in outline a method of procedure which I believe to have demonstrated its value in practice. The general form of the exercise, in which instruction is imparted in the topics of Evolution, Heredity and Variation, deserves a brief consideration. In the teaching of Anatomy, the Laboratory has universally replaced the old-time Anatomical Lecture in the sense that the student's concrete knowledge of structure is fundamentally based on his own personal observation and study. With this alteration in method the lecture in anatomy has exchanged its former place for one occupying a much broader and higher plane. It serves primarily to bring the specialized efforts of the student into a coherent whole, in which the individual objects of his study are viewed from the standpoint of their interdependence, first within the framework of the system to which they belong, and then in the relation of the latter to the entire organism. The morphological detail is acquired by minute personal, and often prolonged and repeated, observation. The summing up of the facts thus acquired, their functional interpretation, their phases of adaptation to the environment of the whole organism, are properly within the domain of the lecture. Within this domain appropriate use can be made of unusual and special illustrative material ordinarily not accessible to the student, or of special methods of demonstrating material habitually used by him in his own laboratory work, such as corrosions, reconstructions, special sections, Roentgen plates, etc.

It is here likewise that the enormous value of the aid afforded to the medical student by Comparative Anatomy can best be

utilized, in throwing its strong side-light on the difficult and often obscure details of human structure. The densely crowded medical curriculum of the present day does not permit the student to engage in systematic and practical work in Comparative Anatomy. And yet there is no region or part of the human body which is not more readily and permanently comprehended through the comparison with the corresponding structures in other vertebrates. It is perhaps the most important single function of the anatomical lecture to bring the salient points of this general relationship of vertebrate organization clearly and succinctly before the student. In this sense I believe that the problems which we are considering this morning are also best presented at the proper point in the anatomical course in fully illustrated lectures to the entire class or to large sections thereof.

For practical reasons I find it advisable to deal with the subject matter of this instruction in two general divisions, as determined by the character, distribution and use of the material employed by the student in his anatomical work. I hence correlate the more generalized considerations to two parts of the regular anatomical teaching, taking up first the subject of Inheritance and subsequently the problem of Variation and Evolution.

1. INHERITANCE

In the ordinary course in General Embryology the student is carried, to a large degree as a review of his undergraduate work, through the morphology of the cell, the mechanism of mitotic cell-division, the behavior of the chromosomes, the origin and differentiation of soma- and germ-cells, the maturation of the latter, and the processes of fertilization and cleavage. These are all phases of cellular life and activity readily and abundantly accessible to each individual student, and mastered by him through close personal observation. This is the proper point in his course for the introduction of the more generalized interpretation of the processes observed. The purpose of this exercise is to translate in the student's mind the more purely mechanical concepts of the vital processes, obtained by his personal study, into terms of their broader significance, viewed from the stand-

point of the cells of the single organism in their physico-chemical aspect and of the entire individual in relation to the race of which he is a unit. These considerations form the introduction to the study of Heredity. They include such topics as the specificity and individuality of the chromosomes, the distribution of paternal and maternal chromatin in syngamy, the theoretical analysis of chromosomal organization in respect to inheritance, the significance of equational and reducing division, the duplex character of the zygote in contrast to the simplex character of the gamete, sex determination. This leads directly to a concise but fairly comprehensive consideration of the laws of Mendelian inheritance, based on the following principles:

1. The existence of unit-characters, interpreted on the factorial hypothesis.

2. Dominance and Recession, in cases where the parents differ in a single genetic factor.

3. Segregation of the contrasting characters in the gametes of the offspring.

4. Independent assortment of contrasting unit-characters in cases where the parents differ in two or more genetic characters.

The Mendelian examples can, of course, be selected from a wide range, according to the material available. In general it is desirable, in view of the student's collateral reading, to employ the cases quoted frequently in the most accessible literature. To illustrate the first three of the above principles any of the following crosses may be used to advantage:

Red and white *Mirabilis* (Correns).

Yellow and green peas (Mendel).

Black and white guinea pig (Castle).

Vestigial and long-winged *Drosophila* (Morgan).

The fourth principle, the inheritance of two or more independent pairs of factors, may be conveniently illustrated by the Mendelian example of cross-fertilization of round yellow with wrinkled green peas, or Morgan's case in which a gray vestigial *Drosophila* is mated with a long-winged ebony fly.

Sex-linked inheritance is illustrated by the transmission of the white eye in *Drosophila* (Morgan), or by the analysis of heredi-

tary color blindness in Man, through each of the parents. This leads to a brief discussion of Mendelian inheritance in Man, with particular reference to the constantly growing importance of Mendelian teratological and pathological human characters, especially in the eye and nervous system.

The aim of the foregoing presentation is to emphasize the fact that the study of the chromosomal assortment furnishes a mechanism which exactly fulfills the Mendelian requirements of pairing in the zygote and subsequent segregation in the gamete, and that in the gametic coupling or linkage the factors carried by the same chromosome tend to remain associated and are hence inherited together.

In the teaching of medical students there is a certain advantage in drawing the illustrations as far as possible from mammalian sources, and for this reason it is desirable, in problems of heredity, to use as fully as may be feasible the rodent examples of guinea pigs, rabbits and mice grouped by W. E. Castle in his book on 'Heredity in Relation to Evolution and Animal Breeding' ('13).

Recently Dr. Helen King of The Wistar Institute of Anatomy has suggested to me the value of the teaching material furnished in this respect by the Rat Colony of the Institute.

2. VARIATION AND EVOLUTION

Following the consideration of the topic of heredity and its physical basis, which occupies a place in the general embryological course, I consider it desirable, preparatory to the study of evolutionary theories, to next present somewhat thoroughly the general problem of *adaptation*, as illustrated by concrete examples presenting themselves to the class in the regular anatomical course. The choice of the topic or topics used for this purpose is of course an extremely wide one, depending largely upon the arrangement of the time and material in the anatomical course of individual institutions. In my own practice I find it useful to introduce a general consideration of the vertebrate shoulder girdle at a point where the student has worked through the development and structure of bone and the forms of ossification in the histological course.

I may here be permitted to give an outline of the ground covered in this exercise for the purpose of affording an example of the range of the presentation and of the amount and kind of the illustrative material required. The accompanying figures are of preparations in the Morphological Museum of Columbia University used in the demonstrations. The topic connects organically with the subject matter of the histological course by beginning its consideration with the unique type of ossification found in the ontogeny of the mammalian clavicle and of the corresponding elements where they occur in the remaining vertebrate classes. This finds its explanation in the phylogenetic history of the bone, originally an exoskeletal derivative introduced secondarily into the complex of the primordial pectoral girdle, in response to the latter's adaptation to definite functional and mechanical requirements. As such it is the first bone of the skeleton to ossify, its primary centre developing in Man during the sixth week, when, at a point corresponding to the middle of the shaft of the future clavicle, a bony nucleus develops directly from the indifferent embryonic mesenchymal skeletogenic tissue, without the appearance of a preformed cartilaginous model. From this central ossific nucleus cartilage subsequently extends mesad and laterad, both toward the sternum and toward the acromion. In this cartilaginous rod, divided by the primary bony nucleus into a sternal and an acromial segment, the rest of the clavicle develops. Late in development (Man, 20th year) a secondary centre appears in the sternal extremity, joining the shaft in the 25th year.

This ontogenetic history of the mammalian bone calls for the consideration, from the standpoint of adaptation and evolution, of three main facts, which bespeak the relation of the mammalian clavicle to homologous skeletal elements in the lower vertebrates:

1. The early direct dermal type of development of the primary clavicular ossific centre.
2. The derivation of the cartilaginous bed in which the rest of the shaft of the bone develops.

3. The mechanical conditions established in the pectoral girdle by the introduction of the clavicle.

The consideration of these topics is based on a study of the following series of types:

1. The primordial vertebrate pectoral girdle is illustrated by the structure in the Elasmobranchs. Any one of our common and readily obtainable Dog-fish, Sharks or Rays will answer the purpose. The simple horse-shoe shaped cartilaginous arch of the girdle in *Squalus acanthias* is shown in fig. 1. The division of the same in the higher forms into a dorsal scapular and ventral coracoid segment, meeting at the point of attachment of the anterior extremity, is foreshadowed in the figure by the use of the colour scheme adopted in the remainder of the series.

The coracoid portions of opposite sides are continuous across the ventral mid-line in a clear hyaline suture. The right and left dorsal or scapular segments of the primitive arch are separated from each other by an interval and their free termination is tipped by a hyaline zone suggesting the supra-scapular cartilage of the later types.

The Elasmobranch pectoral girdle furnishes the primordial fundament upon which all other vertebrate modifications are built.

2. In the Dipnoeans, Ganoids and the modern Teleosts, the primitive uniform cartilaginous girdle begins to become altered in two directions.

1. It is divided into segments.

2. The cartilage is largely replaced by bone from two sources:

a. Intracartilaginous ossification of the primitive girdle segments.

b. Deposit of membrane bone of dermal origin forming the *clavicles*.

A Teleost girdle is shown in fig. 2.

The primary continuous and single elasmobranch girdle is here divided into separate and distinct right and left pectoral arches, each composed of a dorsal scapular and ventral coracoid element. These ossify partly by intracartilaginous replacement, partly by a deposit of membrane bone derived from the dermal



Figure 1. Shoulder-girdle of *Squalus acanthias*, the Dog fish. In the continuous and single pectoral arch of this form the division into dorsal scapular (sc) and ventral coracoid (co) segments of the higher types is foreshadowed on the right half of the girdle by the use of the following color scheme adopted in the rest of the series:

Scapula.....	yellow
Coracoid.....	blue
Epicoracoid.....	brown
Clavicle.....	red
Episternum.....	green
Sternum.....	white

Dr—Dermal horny rays. *Prp*, *Msp*, *Mtp*,—the three basal pieces of the fin, Propterygium, Mesopterygium, Metapterygium. *Ra*—cartilaginous rays (radialia) of fin. *Pct*—continuous undivided pectoral arch.

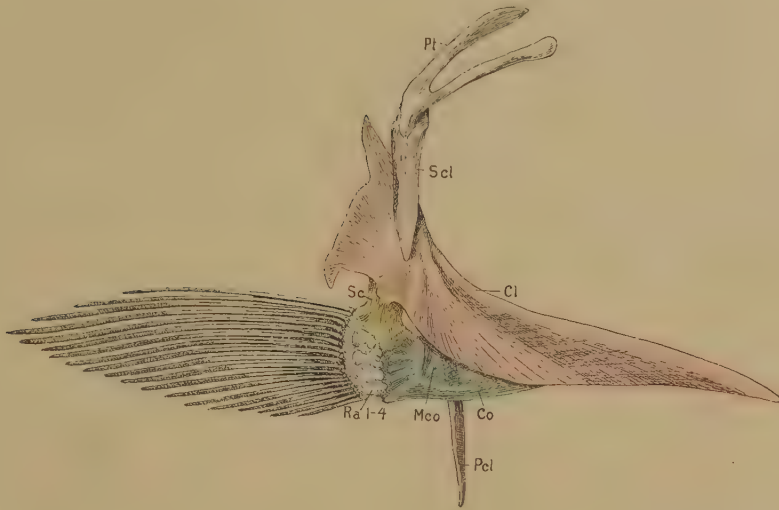


Figure 2. Right shoulder-girdle of *Gadus callarias*, the Cod fish, lateral view. *Cl*—Clavicle (Cleithrum). *Co*—Coracoid. *Mco*—Mesocoracoid. *Pcl*—Post-clavicle (Post-cleithrum). *Pt*—Post-temporal, articulating with epiotic and pterotic processes of skull. *Sc*—Scapula. *Scl*—Supra-clavicle (Supra-cleithrum). *Ra 1-4*—Proximal Radials (Pterygiophores).

exoskeleton and forming the *clavicular* or *cleithral* complex (cleithrum, post- and supra-cleithrum). These investing bones are highly developed in the Teleosts and are connected by a branched bone, the post-temporal, with the epiotic and opisthotic regions of the cranium. In the higher vertebrates they become reduced, furnishing the investing bone of the clavicle and the episternum.

The elasmobranch therefore visualizes the formation of the primitive cartilaginous vertebrate girdle, the teleost the secondary engrafting on a portion of the same of an investing element, the *clavicle*, dermal in origin. This furnishes the outline for the interpretation of the ontogeny of the mammalian clavicle, developing partly by direct, partly by replacing ossification. Thus in the degree to which in higher vertebrates the clavicle enters into direct and intimate relation with the primitive segments of the pectoral girdle, cartilage of coracoid origin becomes added to the primary bony clavicle, enabling it to assume secondary and functionally

important relations to the earlier elements of the arch. The primitive coracoid responds in a very definite manner in making provision from its own substance for the cartilaginous matrix upon which the dermal investing bone of the clavicle is grafted.

The primitive expanded single ventral coracoid plate divides, by the development of one or more fenestrae, into a caudal larger element, the *coracoid proper*, and a cephalic narrower bar, the *procoracoid*, which is invested and replaced by the clavicle. This process is beautifully illustrated in

3. THE ANURE AMPHIBIANS

Example: *Rana catesbiana*, the Bull-frog.

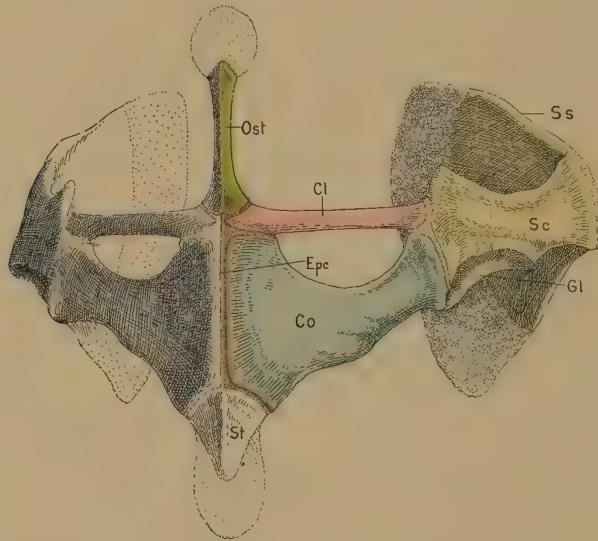


Figure 3: Shoulder-girdle of *Rana catesbiana*, Bull-frog. Cl—Clavicle. Co—Coracoid. Epc—Epicoracoid. Gl—Glenoid cavity. Ost—Omosternum (Epi-sternum—). Sc—Scapula. Ss—Suprascapula. St—Sternum.

The pectoral arch is here formed by two scapular segments, the ventral scapula proper and the more dorsally situated suprascapula, both ossified in cartilage, with the exception of the area along the vertebral margin of the dorsal suprascapular segment which remains in cartilage, frequently impregnated with lime

salts. The cartilaginous coracoid, which meets the scapula in the formation of the glenoid socket, is divided into a caudal element, the *coracoid proper*, and a cephalic bar, the *procoracoid*. The former ossifies, the cartilaginous precoracoid rod is replaced by the investing bone of the *clavicle*.

The amphibian further shows the first appearance of the *sternal apparatus* in association with the pectoral girdle, and of the *epicoracoid*. The latter represents the beginning of a loosening of the originally firm ventral connection of the coracoid, made possible, and of distinct functional advantage in swimming forms, such as the frog (vide infra), by the mechanical substitution of the clavicle in place of a considerable segment of the coracoid. Just as the division of the original single and massive coracoid plate into a cephalic procoracoid and a caudal coracoid in the narrower sense occurred through a transverse split or fenestration in the long axis of the arch, so a similar cleft, at right angles to the preceding, resulted in the separation of the primitive coracoid plate into a lateral scapular coracoid and a medial sternal epicoracoid. In some forms (Lacertilia, Chelonia) the epicoracoid remains cartilaginous or fibro-cartilaginous. It is probably represented in man by the sterno-clavicular fibro-cartilage. In the general significance of its development it may be interpreted as one of the preliminary stages in the detachment of the rigid coracoid from its firm ventral sternal connection and its functional replacement by the more mobile ventral clavicular component of the girdle, while the reduced lateral portion of the coracoid is necessarily retained as the coracoid process, since it forms, at its junction with the scapula, an essential element of the glenoid socket. (Cf. infra, p. 378 and Fig. 12.)

4. REPTILES

The pectoral arch defaults in the Ophidia with the total suppression of the fore limb. In the remaining orders of the class it is found in three forms:

A. The girdle in the Lacertilia is very fully developed.

Example: *Iguana tuberculata*, Iguana (Fig. 4). It is composed of scapula and suprascapula, multifenestrated coracoid and epi-

coracoid and clavicles. The medial extremities of the latter are supported by a T-shaped Episternum, derived ontogenetically by the direct ossification of a dermal anlage, without cartilaginous praeformation. The combination of these components is in direct line with the conditions obtaining in the Monotremes. These, the most primitive mammals, possess among the other structural characters carried over from their reptilian ancestry, a pectoral girdle which conforms closely to the Lacertilian type of the modern saurian reptiles just described. The massive coracoid

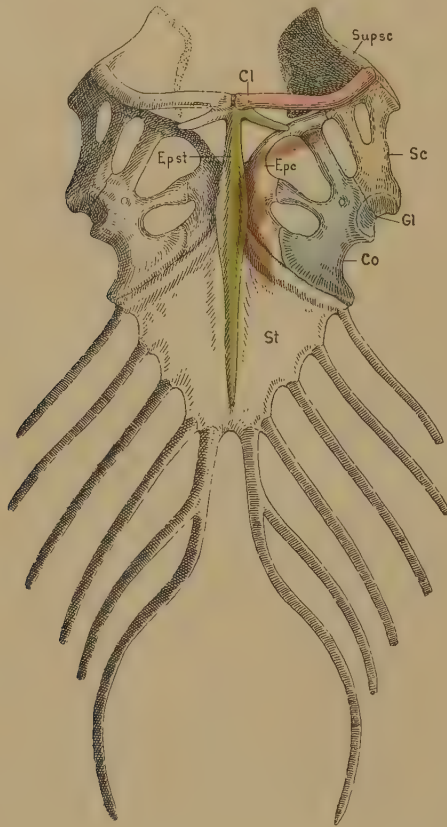


Figure 4. Shoulder-girdle of *Iguana tuberculata*, the Iguana. Cl—Clavicle. Co—Coracoid. Epc—Epicoracoid. Epst—Episternum. Gl—Glenoid cavity. Sc—Scapula. St—Sternum. Supsc—Suprascapula.

extends to the lateral manubrial angle and carries a broad bony epicoracoid plate. The ventro-medial portion of the epicoracoids is covered by the vertical branch of the strong episternum, whose horizontal divisions support the clavicles.

Example: *Platypus anatinus*, Duck-billed Platypus (Fig. 5).

A comparison of figs. 4 and 5 will show at once the transmission of the reptilian character to the primitive mammalian girdle.

B. Within the profound modifications of the exoskeletal apparatus of the Chelonians resulting in the development of the carapace and plastron, the pectoral girdle of these reptiles consists

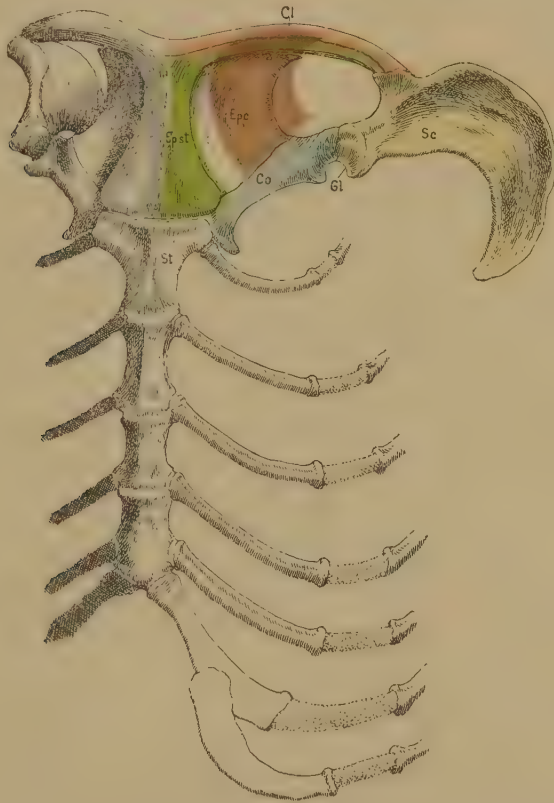


Figure 5. Shoulder-girdle of *Platypus anatinus*, the Duck-billed Platypus. Cl—Clavicle. Co—Coracoid. Epc.—Epicoracoid. Epst—Episternum. Sc—Scapula. St—Sternum.

of the straight dorsal scapular bar joined at the humeral articulation to the ventral coracoid. This is divided by a single large fenestra into the caudal coracoid proper and the cranial procoracoid, whose ventral extremities are joined by the fibrocartilaginous epicoracoid.

Example: *Chelydra serpentina*, Snapping turtle. (Fig. 6.)

C. In the Crocodilians a simple Coraco-scapular arch is developed, the two components meeting in the formation of a glenoid cavity. The coracoid forms a single plate, broadening ventrad and firmly connected to the lateral sternal margin.

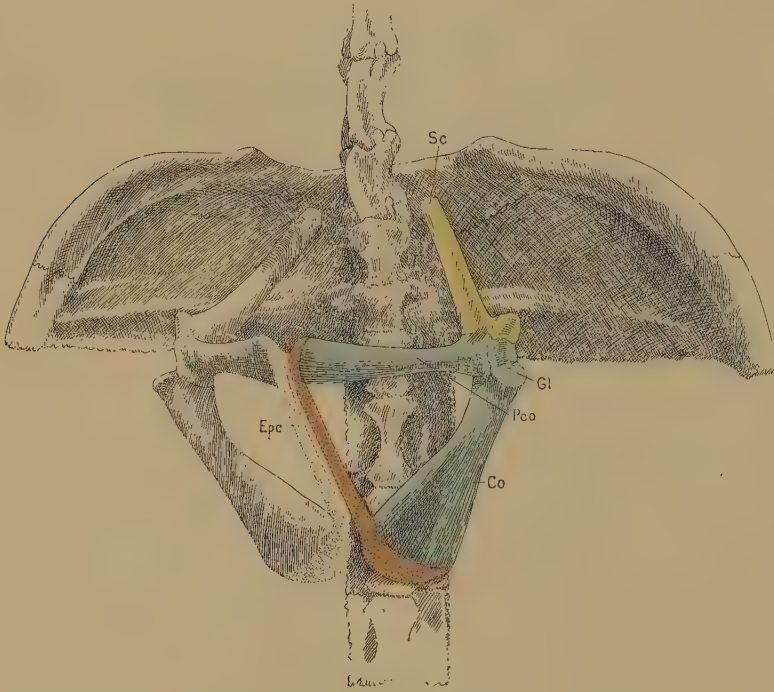


Figure 6. Shoulder-girdle of *Chelydra serpentina*, Snapping Turtle. Co—Coracoid. Epc—Epicoracoid. Gl—Glenoid cavity. Pco—Procoracoid. Sc—Scapula.

Clavicles do not develop, but a ventral episternum makes its appearance. With the additional introduction of a clavicular (furcal) apparatus the crocodilian girdle would connect directly with the avian type. [Cf. figs. 7 and 8]

Example: *Alligator mississippiensis*, American Alligator (fig. 7).

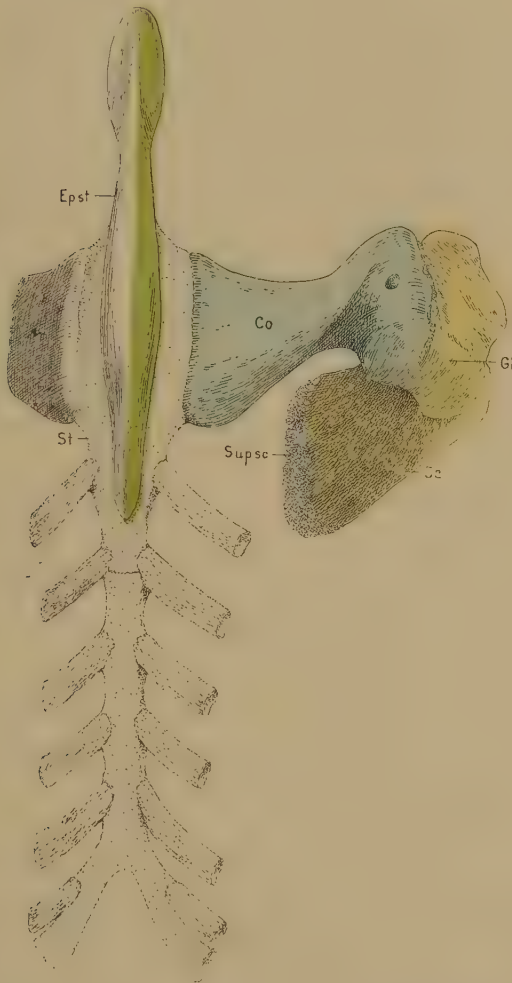


Figure 7. Shoulder-girdle of *Alligator mississippiensis*, Alligator. Co—Coracoid. Epst—Episternum. Gl—Glenoid cavity. Sc—Scapula. St—Sternum. Supsc—Suprascapula.

5. THE AVIAN GIRDLE

In the typical flying birds the slender sword-like scapula is joined at the glenoid to a massive coracoid, which, expanding ventrally, is firmly invaginated in the marginal groove of the broad and carinated sternum. The two clavicles form by fusion of their medial extremities the well-known arch of the *Furcula* or *Wishbone*. The bony Episternum is replaced, at least functionally, by the extensive clavi-sternal aponeurotic membranes. The entire apparatus speaks for two functional adaptations of the girdle structures:

1. The high development of the coracoid in contrast to the comparatively insignificant and slender scapula indicates the preponderance which the ventro-appendicular muscles have obtained over the dorsal musculature as the result of the specific adaptation of the former to the movements of flight. The clavicles (furcula) appear introduced as an additional thoraco-humeral brace against the adduction of the forelimb to the thorax in the action of the pectoral group.

2. The requisite area for pectoral muscular attachment is obtained by the increase in breadth and length of the sternum and by the development of the *Carina* from its ventral surface. Additional surface or muscular attachment is further furnished by the furcula and the episternal apparatus of the interfurcular and sterno-furcular aponeuroses.

Altogether the pectoral girdle of the typical bird furnishes the clearest example of the modification in structure and relation of the components correlated to specific functional adaptation.

Example: *Olor buccinator*, the Trumpeter Swan. (Fig. 8).

The primitive vertebrate shoulder-girdle, composed of its phylogenetically oldest elements, scapula and coracoid, is characterized by the great firmness of the ventral coracoid connection, and is from its construction rigid and nearly immobile. A girdle of this type, combining great strength and rigidity, enables a powerful ventro-appendicular musculature to move the anterior limb within a limited range in a few directions with great force, but is not adapted to a wider extent of more diversified motion.

It is chiefly of value in permitting movements of adduction and rotation with a free extremity, without carrying the limb against or across the thorax, as in the acts of swimming, flying or digging. In these a rigid pectoral girdle and firm coraco-sternal junction act as a supporting arc, keeping the shoulder and gleno-humeral articulation away from the thorax and preventing undue adduction of the extremity, while permitting the full unfolding of the pectoral muscle-action.



Figure 8. Shoulder-girdle of *Olor buccinator*, Trumpeter Swan. *Ca*—Carina of sternum. *Co*—Coracoid. *Fu*—Furcula (Clavicles). *Gl*—Glenoid cavity. *Sc*—Scapula. *St*—Sternum.

This type of shoulder girdle hence occurs in forms in which the forelimb is used in a limited number and range of forcible movements of ab- and adduction and rotation.

It occurs, with or without the introduction of the secondary clavicle, in Elasmobranchs, Teleosts, Reptiles, Birds and Monotremes, in the latter as a direct reptilian inheritance.

Examples used in the illustration of the coracoid element:

<i>Squalus acanthias</i>	Figure 1
<i>Gadus callarias</i>	Figure 2
<i>Rana catesbiana</i>	Figure 3
<i>Alligator mississippiensis</i>	Figure 7
<i>Iguana tuberculata</i>	Figure 4
<i>Chelydra serpentina</i>	Figure 6
<i>Olor buccinator</i>	Figure 8
<i>Platypus anatinus</i>	Figure 5

MODIFICATIONS OF THE PRIMITIVE SCAPULO-CORACOID ARCH

1. The primary firm sternal connection of the coracoid is loosened in one or both of the following ways:

A. Axial fenestration of the coracoid, either multiple (*Iguana*, *Monotremes*) or single (*Rana*, *Chelonia*), resulting in its division into a posterior or caudal element, the *Coracoid proper*, and an anterior or cranial bar, the *Procoracoid*.

Examples: *Rana*, fig. 3, *Iguana*, fig. 4, *Platypus*, fig. 5, *Chelydra*, fig. 6.

B. Transverse division, at right angles to the preceding, of the primitive coracoid into a lateral scapular segment, entering into the gleno-humeral articulation, and a medial sternal element, the *Epicoracoid*. The latter may ossify as a separate bony element, of the girdle, or may remain as a fibro-cartilaginous plate, thus still further increasing the mobility of the coraco-sternal connection.

Examples of *Epicoracoid* cited:

<i>Rana</i>	Figure 3
<i>Iguana</i>	Figure 4
<i>Chelydra</i>	Figure 6
<i>Platypus</i>	Figure 5

2. The coracoid may be further reduced, losing its medial connection altogether and appearing as a relatively insignificant process of the scapula, but always retained in extant forms as the Coracoid Process (subcoracoid centre) because the glenoid socket is always formed by both scapula and coracoid, no matter how far the reduction of the latter may be carried.

This reduction of the coracoid obtains in all mammals, except the Monotremes, which retain the full development of the reptilian coracoid with sternal connection through the epicoracoid. In some Marsupials, the next order above the Monotremes, the strong coracoid reaches the sternum during the early ontogenetic stages, but becomes reduced in later development to the coracoid process. Thus in *Trichosurus*.

In some forms (Man) the original path of the sternal extension of the coracoid is indicated by bands of fibrous tissue, containing at times fibro-cartilaginous nodules, forming the *Costo-coracoid ligament*. (Cf. Plate I, fig. 1)

3. The primitive scapulo-coracoid arch may be further modified by the introduction of the clavicle, a bone derived from the tegmentary exoskeleton and secondarily added to the primary elements of the girdle by investing the cranial portion of the coracoid (procoracoid). This addition of the clavicle may occur in two forms:

A. The clavicle replaces the procoracoid in the ventral segment of the pectoral arch, while the remaining original components, viz. Caudal Coracoid, Epicoracoid, and Episternum are retained in their full development. In this case the clavicle is introduced for the purpose of adding to the strength of the ventral arch of the girdle and of increasing the surface for attachment of the pectoral musculature by the development of extensive aponeurotic membranes between the clavicles and the other elements of the girdle and the sternum (Carnate Birds, Monotremes).

In the birds in which the wing muscles are relatively reduced the clavicles become diminished in size and strength, lose their direct sternal apposition and the union with the opposite bone in the furcular junction.

Example: *Ramphastos ariel*, the Toucan. (Fig. 9).

In the Brevipennate flightless ostriches the bone defaults altogether, only the coracoid remaining in *Struthio*, *Rhea* and *Casuaris*. This speaks for a relatively late acquisition of the clavicle as a component of the Avian Girdle.

Example: *Casuaris casuaris*, the Cassowary. (Fig. 10).



Figure 9. Shoulder-girdle of *Ramphastos ariel*, the Toucan. *Cl*—Reduced clavicles. *Co*—Coracoid. *Gl*—Glenoid cavity. *Sc*—Scapula. *St*—Sternum.

In one ostrich, *Dromaius*, the Emu (Fig. 11) rudiments of the separate clavicles remain as two small bony crescents loosely attached to the girdle.

In the South American group of the Crypturi, although the sternum is keeled and the wings are to a certain extent functional, yet the shoulder girdle and sternum have a distinct struthious character. This, together with other anatomical features, places these small ground-birds with the Ostriches in the super-order of the Dromaeognathae.

B. The clavicle, secondarily engrafted on the procoracoid element of the primitive girdle, functionally replaces the caudal coracoid proper, which becomes reduced to the lateral portion entering, as the coracoid process of the scapula, into the construction of the glenoid socket for the humeral articulation.



Figure 10. Shoulder-girdle of *Casuarius casuarius*, the Cassowary. Co—Coracoid. Gl—Glenoid cavity. Pco—Procoracoid. Sc—Scapula. St—Sternum.

Thus in the unique ontogeny of the mammalian clavicle, the primary direct centre of ossification of the shaft, appearing without the preceding formation of cartilage, in the human embryo in the sixth week, represents the dermal element of the bone, derived from the exoskeleton. The cartilage added to this pri-

mary centre at both the sternal and scapular ends is derived from the cranial element of the primitive coracoid, the procoracoid, and forms the bed in which further ossification of the shaft of the bone proceeds in both directions. The acromio-clavicular fibrocartilage and the sternal epiphysis of the clavicle, whose secondary centre develops in Man between the 18th and 20th year and joins



Figure 11. Shoulder-girdle of *Dromaius novae-hollandiae*, the Emu. *Cl*—Rudimentary clavicles. *Co*—Coracoid. *Gl*—Glenoid cavity. *Pco*—Procoracoid. *Sc*—Scapula. *St*—Sternum.

the shaft in the 25th year, are likewise part of the cranial procoracoid element. The lateral portion of the caudal coracoid proper constitutes the coracoid process of the scapula, completing with its subcoracoid centre (10th year) the glenoid fossa. (Fig. 12.)

The rest of the mammalian caudal coracoid defaults, with the exception of the costo-coracoid ligament and its occasional fibrocartilaginous nodules. (Plate 1, fig. 1.)

The sterno-clavicular fibro-cartilage is also a derivative of the primitive coracoid, and may be interpreted as part of its medial or sternal extremity or as an epicoracoid (Lacertilia, Monotremes).

The human interclavicular ligament and the occasional ossicula superasternalia (fig. 13) are referable to persistent rudiments of the primitive episternum. The introduction of the clavicle,



Figure 12. Human scapula, 14th year. *Co*—Coracoid. *Sco*—Subcoracoid.

replacing in the mammalia above the Monotremes the larger ventral portion of the coracoid and forming the thoracic connection of the pectoral girdle, influences the disposition of the pectoral musculature. In the superficial ectopectoral sheet the clavicle affords origin to the clavicular portion of the Pectoralis major. The cephalic part of the deeper entopectoral layer furnishes in non-claviculates the generalized Sterno-chondro-scapularis, which, with the appearance of the clavicle, becomes in its central segment the mammalian Subclavius, while its medial portion is converted into the costo-clavicular or rhomboid ligament, and its lateral fibres become the coraco-clavicular ligaments (conoid and trapezoid) (fig. 16).

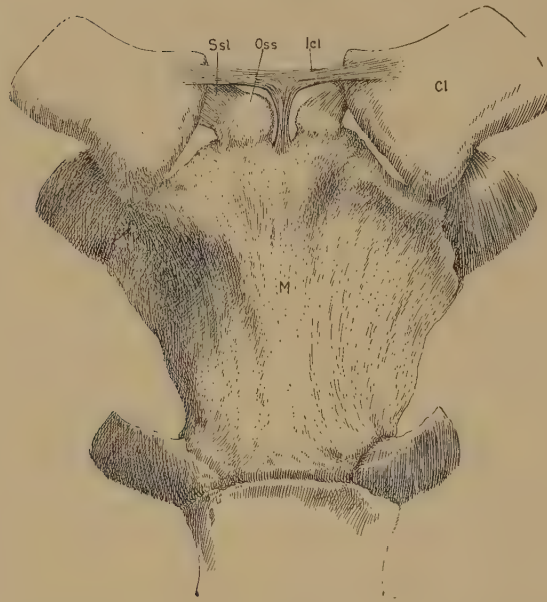
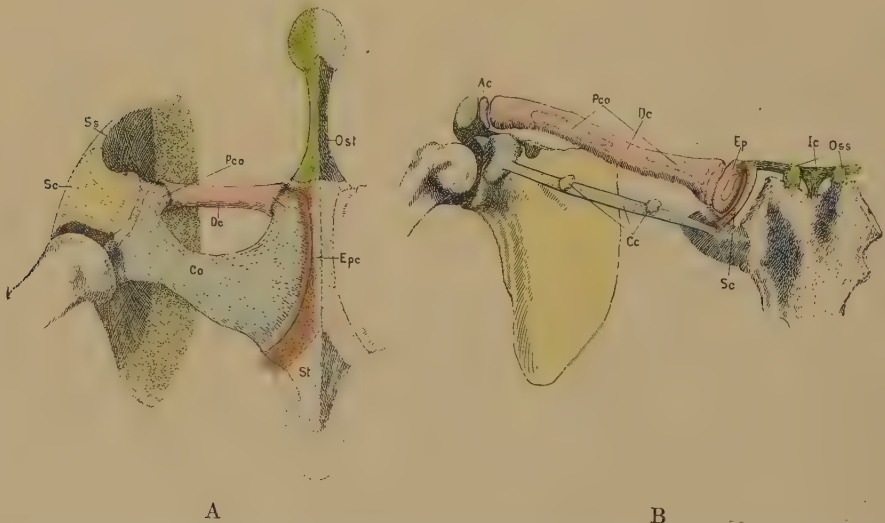


Figure 13. Human adult, Sternum and Ossicula Suprasternalia, with Interclavicular and Suprasternal ligaments. *Cl*—Clavicle. *Icl*—Interclavicular ligament. *M*—Manubrium. *Oss*—Ossa suprasternalia. *Sst*—Suprasternal ligament.



Figures 14 *A* and 14 *B*. Schema of evolutionary derivation of human pectoral girdle from the vertebrate ground-plan, as illustrated by the Anure Amphibian.

The analysis of the human pectoral girdle in reference to the derivation of the component elements reads therefore in tabular form as follows:

ARCHEAL ANLAGE:	COMPONENTS of HUMAN PECTORAL GIRDLE
Primordial cartilaginous Girdle of Elasmobranchs	} Scapula and Coracoid
Dermal Cleithrum and Clavicles of Teleosts	} Primary direct centre of clavicular ossification.
Cranial Procoracoid	{ Cartilage rod on which dermal clavicle is engrafted.
Ventral (Medial) end of Procoracoid	{ Epiphyseal centre at sternal extremity of clavicle.
Epicoracoid	Sterno-clavicular fibro-cartilage.
Episternum	{ Ossa suprasternalia Inter-clavicular and Suprasternal Ligaments.
Dorsal (Lateral) end of Procoracoid.	Acromio-clavicular fibro-cartilage.
Caudal coracoid proper	{ Coracoid Process, Subcoracoid, Costo-coracoid ligament and contained fibro-cartilaginous nodules.
Cranial segment of entopectoral muscle sheet furnishing the sterno-chondro-scapularis.	
a. Lateral portion	{ Coraco-clavicular conoid and trapezoid ligaments.
b. Central portion	Subclavius.
c. Medial portion	Costo-clavicular rhomboid ligament.

Figure 14 A. Plan of pectoral girdle of Anurè Amphibian based on the structure in *Rana catesbiana*. *Co*—Coracoid. *Dc*—Investment of Procoracoid by dermal clavicle. *Epc*—Epicoracoid. *Ost*—Omosternum. (Episternum). *Pco*—Procoracoid. *Sc*—Scapula. *Ss*—Suprascapula. *St*—Sternum.

Figure 14 B. Phylogenetic derivation of elements of the human pectoral girdle. The homologous structures are indicated in A and B by the corresponding colors. *Ac*—Acromio-clavicular fibro-cartilage. *Cc*—Costo-coracoid ligament and contained fibro-cartilaginous nodules. *Dc*—Primary ossific centre of dermal Clavicle. *Ep*—Sternal epiphysis of Clavicle. *Ic*—Interclavicular ligament. *Oss*—Ossicula suprasternalia. *Pco*—Procoracoid cartilage. *Sc*—Sterno-clavicular fibro-cartilage.

The functional results of these adaptations in the mammalia is to substitute, for the nearly immobile ventral coracoid connection of the pectoral girdle with the sternum, the clavicular apparatus with moveable articulation at both the sternal and scapular extremities. The clavicle acts as a sufficient thoraco-humeral brace, maintaining the position of the glenoid cavity in movements of the anterior extremity against the thorax, while at the same time the articulations at either extremity greatly increase the range and variety of these movements. The clavicle acts as the radius of the arc in which circumduction of the arm takes place, with the centre placed at the mobile sterno-clavicular articulation, while at the same time the lateral claviculo-scapular joint enables the glenoid socket to alter its direction and the scapula as a whole to maintain contact with the curvature of the thoracic wall in different positions.

Both of these mechanical functions of the mammalian girdle would have been interdicted by the retention of the complete primitive coracoid, with its firm ventral attachment to the sternum and the immobile lateral junction with the scapula in the glenoid articulation.

The replacing clavicle thus finds its full development in mammals above the Monotremes, especially in forms which habitually execute forcible movements of the anterior extremity against the thorax. The bone is hence especially strong in mammals using the anterior limb for digging (Edentates), swimming (some Rodents), flying (Cheiroptera), or grasping (Primates).

When the anterior extremity habitually performs no or only slight movements against the thorax, and is used solely as a supporting or progressional limb, the clavicle is reduced or defaults altogether. The pectoral girdle then consists solely of the scapula and its coracoid process and is attached to the thorax only by the thoraco-appendicular muscle planes. The clavicle is thus absent in many Carnivores and in the Ungulates. It is rudimentary in some Rodents and Carnivores (Felidae), appearing as a slight bony or fibrous intersection in the ventral sheet of the cephalo-humeral muscle.

It is significant, in reference to the ontogenetic derivation of the primary clavicular anlage, that in Man, in cases of congenital absence of some of the cranial membrane bones (Parietal), the clavicles, also derived from the investing skeletal tissue, usually likewise default.

The high development of the clavicle in the Primates is the expression of the greater freedom of action of the anterior extremity, especially in movements of ad- and abduction, circumduction and rotation, permitting of a wide range of diverse uses.

The presentation just outlined in the concrete example of the vertebrate shoulder girdle is intended to introduce the student to the consideration of the unity in groundplan of vertebrate organization and of its far-reaching modifications in response to environmental and functional adaptations, and to thus pave the way for his study of the evolutionary problem. The matter contained in the preceding pages can readily be handled within the period of a single anatomical lecture, and the illustrative material is for the most part universally accessible. The only examples used which are more difficult to obtain are the shoulder-girdles of the Monotremes and of the Ostriches, and these can be demonstrated by drawings or photographs. The remaining illustrations are all derived from the dissecting room, the market or the usual range of domestic or laboratory animals. The effort required for their suitable preparation and assembly is, in my judgment, not unwarranted in view of their value from the teaching standpoint.

It goes without saying that practically any portion or region of the body may be selected, instead of the example here given, for the purposes of this presentation, according to the space occupied by it in the anatomical course and the material available. Excellent opportunities for this treatment are afforded by the alimentary canal, especially the gastric and ileo-colic regions, the heart and vascular system, the central nervous system, the phylogeny of the vertebrate respiratory system, the pelvic girdle, the genito-urinary tract, etc.

EVOLUTION AND VARIATION

The general problem of evolution is best approached in the medical curriculum through the consideration of *variation* as forming the physical basis of structural evolutionary change.

The medical student confronts the problem of variation from the outset of his practical medical course and carries it with him throughout the remainder of his professional career. He encounters it during his work in the Dissecting Room in more or less significant instances, which either come under his own personal examination, or under that of his fellow students. It is highly desirable that he should not be led to regard these as mere anatomical curiosities, or as examples of a *lusus naturae* which are inexplicable and devoid of a deep scientific meaning. He meets with variation again in his later, so-called "clinical" years of the course, in his hospital service and in his subsequent practice, often in some of its important semi-pathological aspects. Variation, wherever found, always readily chains his attention and arouses his close interest.

Variation in my experience forms therefore the portal through which the broader theme of evolution can best be approached by the medical student, and I find that he invariably responds to the opportunity for clarifying his concepts of variation along the lines of evolutionary doctrine. I am therefore in the habit of dealing in the anatomical course in the first place with variation along the line of a simple working classification of variants encountered in the human body, to which the student can correlate his own observations, which serves him as a guide in his interpretation of the same, and which can be made the basis for the general theoretical consideration of evolution.

A presentation of this nature should be illustrated as fully as convenient, and I find that the assembly of such material calls for relatively small expenditure of time and effort, considering its educational value. This material is naturally of three kinds and derived from three sources:

1. *Human Variations*. The average dissecting room yields in the course of a few years a surprisingly large harvest of significant and desirable human variants, if they are systematically

preserved. This is of course the main source of the annual increment and the resulting gradual growth of this class of illustrative material. Some of the records can be kept in the form of drawings, charts or photographs. I have, however, found it desirable to make permanent wet or dry preparations of the structures, wherever possible. In the case of the large and important group of the muscular variants I have for many years almost uniformly taken casts, which are subsequently colored and yield admirable and durable teaching objects.

A few desirable illustrations can be obtained by photograph or cast from the living subject, such as hare-lip, hypospadias and other developmental arrests of the genito-urinary region, polydactyly, etc.

2. *Ontogenetic Material.* The comparative embryological collection furnishes an almost unlimited amount of material for the correlated illustration of courses in variation and evolution, and should be utilized to the fullest extent, in slides and particularly in reconstructions.

3. *Comparative Anatomical Material.* A very large number of excellent examples are offered by the domestic and laboratory animals, or by forms readily obtained in the market (fishes, reptiles). The rarer forms are of course only to be obtained gradually and as occasion offers, but pending such acquisition very good use can be made of drawings and photographs.

A CLASSIFICATION OF HUMAN VARIATIONS TO SERVE AS A GUIDE IN
ANATOMICAL INSTRUCTION TO MEDICAL STUDENTS

A distinction is first drawn between two general groups of variants which can, with certain reservations to be subsequently considered, be provisionally defined as: 1. *Ontogenetic Variation* and 2. *Phylogenetic Variation*.

While every variation is in one sense ontogenetic, as resulting from the atypical differentiation of the embryo leading to the development of the abnormal individual, the term is here used to designate those variations which base themselves upon the normal ontogenetic range of the species to which the individual belongs. Ontogenetic variants arise from material forming a normal constituent of the embryo but not carried typically into the adult organization.

It is well-known that the embryo in the early stages contains many structures which disappear or become highly modified during subsequent development. The shift, for example, in the mammalian axial venous system from the primitive bilaterally symmetrical groundplan to the dextral position occupied in the typical adult, affords a fruitful field for the development of variants of this category.

Phylogenetic variations on the other hand are in large part *reversional* reproductions of conditions not found normally in the embryo, marking the hereditary reappearance of characters belonging to the ancestors of the species, but lost or altered in the modern descendants in the majority of the individuals composing the race to-day. A smaller number of phylogenetic variants are *progressive*, constituting examples of evolutionary changes active to-day, and as yet evidenced only in a small minority of individuals.

The numerical disproportion of the progressional and reversional phylogenetic variations results naturally from the fact that the latter draw for their appearance upon the accumulation of the entire past phyletic history of the race, while the former are confined to the limited field in which the extremely slow structural reorganizations are preparing for the next evolutionary step of the future. The questions as to the influence of variation by mutation in evolution is taken up in the subsequent general consideration.

1. *Ontogenetic Variants*

A. ERRORS IN DEVELOPMENT.

1. *Arrest of normal development.*

Examples: Harelip, Cleft palate, Hypospadias, Vesical extrophy, certain instances of Renal dys-topia.

2. *Failure of normal development.*

Examples: Default of the pectoral muscle group; single kidney.

3. *Atypical development of vestigial structures of a transitory character in normal development.*

Examples: Right Aortic Arch and other main Variations of the primary aortal branches in Man.

4. *Atypical development of permanent vestigial structures.*

Example: Usual development of the muscles of the external ear.

5. *Errors in definition of muscular integers.*a. *In Cleavage into successive muscular planes.*

Examples: The group of the intermediate pectoral muscles, Tensor semi-vaginae articulationis humero-scapularis, Pectoralis minimus, Costo-cora-coideus.

b. *In Segmentation into components within the confines of a single muscular plane.*

Examples: The deep Axillary Arches.

c. *In Migration.*

Example: The Sternales.

d. *In Metamorphosis.*

Examples: Mutual relation between Ischio-coccygeus and Lesser Sacro-sciatic ligament, between Levator ani and Obturator fascia.

B. REVERSIONAL ONTOGENETIC VARIANTS.

In these the variation possesses a phyletic significance, but appears in the normal ontogeny of the species and is lost typically in the course of later development.

Example: 13 free ribs.

C. PROGRESSIVE ONTOGENETIC VARIANTS.

Normally developed structures lose their typical relations during later stages, in conformity with an advancing evolutionary process.

Example: Variability of 12th rib and its default as a free skeletal segment by synostosis with the 19th vertebra.

2. *Phylogenetic Variants*

A. REVERSIONAL PHYLOGENETIC VARIANTS.

1. ARCHEAL GROUP, signalized by the appearance of characters belonging to the mammalian ancestry, and hence occurring in fossil and extant reptilia and widely distributed throughout the mammalian phylum.

Example: The ent-epicondylar foramen and the associated skeletal, muscular, arterial and nervous modifications around the distal extremity of the humerus in Man. This constitutes a very constant and characteristic complex of anatomical characters wherever it occurs.

It appears nearly uniformly in the fossil reptilia, and especially in the Permian promammalian forms, and lies clearly in the mammalian ancestral line. It is very generally present in extinct mammalia. In living reptiles the foramen is present in a single form, *Hatteria punctata*. It is absent in birds and variously distributed in the mammalian order. In general it would appear that the arrangement has a functional significance in the use of the anterior extremity, protecting the main brachial or ulno-interosseus artery of the limb and the brachial nerve, which pass through the foramen, against undue pressure in forcible flexion of the forearm on the brachium at the elbow. As such it appears widely distributed among the active and powerful early reptiles, but has been lost, with the single exception of *Hatteria*, in their reduced and creeping modern descendants. It is absent in the bird, because in the single vital use of the forelimb in flight there is no flexion at the elbow. In the mammalia it appears especially

in those forms which use the anterior extremity not merely for progression, but also for the special movements of swimming, digging, and grasping. Thus it has been transmitted to both extant monotremes from their reptilian ancestry, one a swimming form, *Platypus*, the other a digging ant-eater, *Echidna*.

In the *Marsupalia* the foramen is present with the exception of the aberrant polyprodont *Notoryctes*, and the *Dasyuridae*, representing the insectivores and carnivores of the Australian and Papuan zones, (Cf. infra, placental carnivora).

In the *Edentates* the foramen is very generally present in all living forms, with the exception of one species among the Pangolins, *Manis temminckii*, and in the genus *Bradypus* among the Sloths, where, however, one species carries the structure (*Bradypus torquatus*).

The members of the order, which really comprises three non-related types of ordinal rank, the *Tubulidentata* (*Orycteropus*), the *Pholidota* (Pangolins) and the *Xenarthra* (Ant eaters, Armadillos and Sloths), are characterized by the use of the anterior extremity for digging in the myrmecophagous forms, or for arboreal suspension in the Sloths, functions which appear to favor retention and wide distribution of the ent-epicondylar foramen.

In the aquatic mammals, which have modified the anterior extremity into a flipper (*Sirenia*, *Cetacea*, *Pinnipede Carnivora*), the movements of the greatly modified bones of the forearm against the humerus are extremely limited, or interdicted by bony union. The ent-epicondylar foramen is uniformly wanting.

In all the subdivisions of the extensive group of the *Ungulates*, using the anterior extremity solely for progression, the foramen is absent. In the *Rodents*, with great diversity of habit and structure, the humerus is equally variable. The ent-epicondylar foramen is wanting in the majority of the numerous types included in the order.

The *Insectivora* possess the foramen except in a few instances (*Erinaceus*).

In conformity with the adaptation of the anterior limb for flight (cf. supra, humerus of bird) the *Cheiroptera* do not carry the entepicondylar foramen.

Interesting conditions in respect to the development of the foramen occur in the *fissipede carnivora*. In the *cynoid* forms (dogs, jackals, foxes and wolves) and in the *arctoid* bears the foramen is not present. In the *aeluroid* cats and their allies, on the other hand, the structure is uniformly present. *Hyaena*, which in the palaeontological history of the fissipede carnivora appears linked through the eocene *Amphictis* to both the modern *Felidae*, and the *Viverridae*, usually does not carry the foramen. Occasionally traces of the structure appear as individual variation in this form. (Plate II, figs. 1, 2).

Among the *Primates* the foramen is present in all extant *Prosimians*, with the exception of one Lemur, *Perodicticus*, and in the *Platyrrhine* monkeys of the New World, both groups being largely arboreal in habit, with extensive adaptation of the anterior extremity to this mode of life. On the other hand, the foramen is absent in the *Catarrhine* suborder of the old world monkeys, in the *Anthropomorph Apes* and *Man*. In the latter it appears as an archeal type of reversional variation.

A plan of the vertebrate distribution of the ent-epicondylar foramen is shown in figure 15. plates III and IV give a selection of comparative types used in the presentation, and its occurrence in *Man* is illustrated in figure 3 of plate II and in plate V.

2. PROGONAL GROUP. The qualification 'progonal' is intended to designate a variant whose degree of phyletic relationship falls within the limits of the general mammalian organization, in contrast to the first or "archeal" group in which the variant character appears as a heritage derived from the promammalian reptilian ancestry. I have selected for illustration two such cases, in which a muscle forming part of the normal organization in many representatives throughout all mammalian orders, develops atypically in *Man* as a progonal reversional variation in the meaning above defined.

1. The *M. Omo-cleido-transversarius*, or *Levator claviculae* appears as a very widely distributed myological character in the majority of the mammalia.

It arises from the cranial base, or from the transverse processes of one or of several of the upper cervical vertebrae (especially the

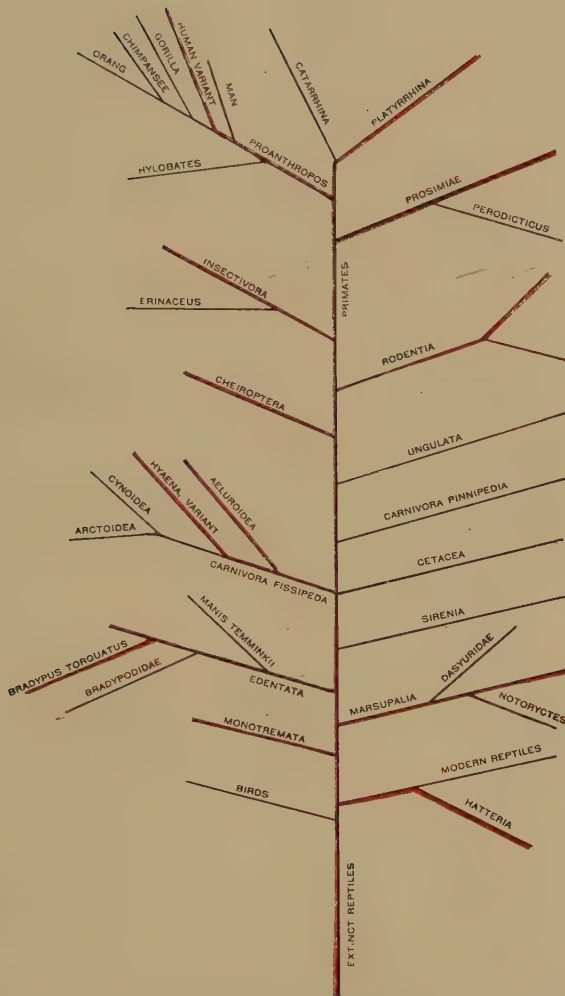


Figure 15. Plan of the phyletic distribution of the ent-epicondylar foramen in vertebrates. The red line shows the presence of the structures involved.

Atlas), descends, usually under partial cover of Trapezius and Sterno-mastoid, and is inserted into the acromion process of the scapula and into the acromial end of the clavicle, when this bone is present. It is supplied by branches of the second to fourth cervical nerves. It occurs as a single muscle, or more rarely divided into a ventral and dorsal slip, in the following mammalia:

Monotremata. Platypus, Echidna.

Marsupalia. Phascogale, Myrmecobius, Dasyurus, Chironectes, Didelphis, Cuscus, Thalacinus.

Edentata. Dasypus, Orycteropus.

Insectivora. Chrysochloris, Gymnura, Erinaceus, Centetes, Solenodon, Myogale, Tupaia, Galeopithecus.

Cheiroptera. Pteropus, Vesperugo noctula, V. murinus.

Rodentia. Dasyprocta, Erethizon, Sciurus, Lepus, Siphneus.

Carnivora. Canis, Felis, Hyaena, Viverra, Genetta, Aeonyx, Cercoleptes, Paradoxurus, Phoca.

Ungulata. Sus, Bos, Ovis, Hyrax, Hippopotamus.

Cetacea. Globiocephalus, arising from Atlas with insertion into fascia of Supra- and Infraspinatus.

Primates.

Prosimiae: Loris, Nycticebus.

Simiae: Macacus, Cercopithecus, Innus, Cynocephalus, Ateles Anthropolomorpha.

The muscle has been found wanting only in the following forms:

Edentata: Bradypus, Myrmecophaga, Tatusia.

Insectivora: Condylura, Talpa.

Chiroptera: Plecotus.

Prosimiae: Perodicticus.

It is therefore one of the most generalized of mammalian muscles, appearing in both extant Monotremes, in the Marsupalia and in many representatives of all the Monodelphian orders, with the exception of the Sirenia.

Plate 6 shows the muscle appearing in Man as a phylogenetic reversional variant of progonal rank.

The normal occurrence of the muscle in one of the lower Primates is shown in plate VII, fig. 1.

2. M. Sterno-costo-scapularis. In mammalia the cranial portion of the entopectoral muscle sheet comes into relation with the

shoulder girdle. In its primitive form it appears as the Sterno-chondro-scapularis or Sterno-costo-scapularis, extending from the manubrium of the sternum and the cartilage or bone of the first rib to the coracoid process and the adjacent cranial border of the scapula. As such it occurs widely in the non-clavicate mammals, with the exception of the forms adapted to aquatic life, Cetacea, Sirenia and Pinnipede carnivora.

With the introduction of the clavicle the sterno-scapularis gains an intermediate attachment to this component of the girdle and is thus divided into a proximal portion extending from the sternum to the clavicle, and a distal segment passing between the clavicle and the coraco-scapula.

In the lower clavicate mammals this leads in all orders to a great diversity of the details in the arrangement of the muscle, as indicated by the terminology applied to the individual components, as Sterno-coracoideus, Costo-coracoideus, Scapulo-clavicularis, Scapulo-costalis minor, Retroclavicularis, Supracoracoideus, Pectoralis longus, and, where the primitive humeral insertion of the entopectoral layer, from which the muscle derives, is retained (Monotremes), Epicoraco-humeralis or ventral Deltoideus.

In many forms, and typically so in Man and the Primates generally, the proximal portion of the generalized Sterno-scapularis, between the thoracic parietes and the clavicle becomes the Subclavius, while the distal segment passing from the clavicle to the coracoid process metamorphoses into the coraco-clavicular (conoid and trapezoid) ligaments.

At times in the human subject the original continuity of the two structures is revealed by the insertion of the lateral subclavian muscle fibres into the coraco-clavicular ligament. Occasionally they reach in this way the base of the coracoid or even the adjacent portion of the cranial scapular margin.

[Plate I, fig. 2. Coracoid insertion of Subclavius in Man.]

In some instances in Man the reversion is more complete, and the Sterno-scapularis appears in its primitive form, either replacing the typical human subclavius or occurring in conjunction with a more or less modified subclavian derivative from the entopectoral layer. These latter cases are usually recorded in the

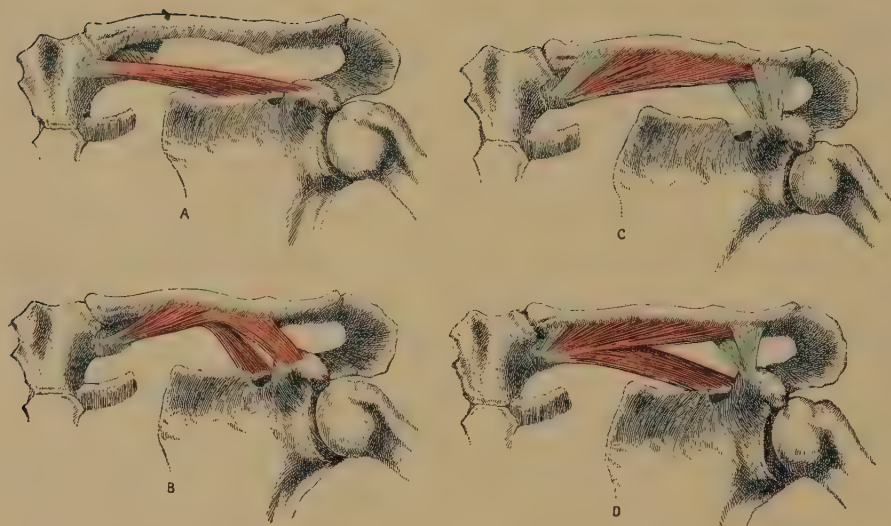


Figure 16. Schemata showing the effect of the introduction of the clavicle on the disposition of the M. Sterno-costo-scapularis.

A. Primitive condition. M. Sterno-costo-scapularis, as it occurs in non-claviculate mammals and in the human variant, without attachment to the clavicle.

B. The central portion of the muscle acquires a secondary attachment to the clavicle, resulting in the establishment of two derived muscles, the Costo-clavicularis and Coraco-clavicularis.

C. Typical condition in Man. Some of the proximal fibres of the Costo-clavicularis metamorphose into the Rhomboid ligament, the main portion of the muscle becomes the Subclavius and the Coraco-clavicularis furnishes the Conoid and Trapezoid ligaments.

D. Human variant. The normal Subclavius and Clavicular ligaments are associated with a Costo-scapularis.

literature as instances of "reduplication of the subclavius." An example of the Sterno-scapularis replacing the subclavius in Man, as a progonal reversional variant, is shown in plate VIII. The muscle as it occurs normally in combination with the Omocleido-transversarius in one of the platyrrhine monkeys, *Ateles ater*, is shown in figure 2, of plate VII.

3. ATAVAL GROUP. The term "ataval" is here used to designate a more direct ancestor, an "atavus" or grandfather, in contradistinction to a more distant forbear, the "progonus." The variants of this group derive from the common Primate stem, and, when they occur in Man, represent either reversions to the Proanthropoid ancestor common to Man and the Anthropomorph Apes, or more distantly to the general Primate organization. With the shortening of the evolutionary path between the human variants of this type and their phyletic source, their number and the frequency with which they appear naturally increases. Hence the majority of the human reversional variations naturally fall within this group. To instance only a few of the many examples the following may be cited:

Axillary arches of pannicular derivation.

Pectoralis quartus.

Chondro-humeralis.

Scansorius.

Dorso-epitrochlearis.

Union of condylar head of Flexor sublimis with Flexor profundus digitorum.

Default of Peroneus tertius.

Arrest of pelvic advance at 26th vertebra.

From the mass of the available examples I have here selected two for more detailed consideration and illustration.

1. *Humeral Insertion of the Pectoralis Minor.*

With few exceptions, depending on individual variation, the Pectoralis minor and Pectoralis abdominalis of the Prosimiae and of both the catarrhine and platyrrhine groups of the lower monkeys insert into the capsule of the shoulder joint and through its fibres into the radial tuberosity and the adjacent lateral surface of the shaft of the humerus, under cover of the Pectoralis major

(Cf. plate VII, fig. 2). With or without an associated axillary arch the tendon forms part of the deep layer of the common pectoral tendon of insertion. In the anthropoid apes and in Man the insertion of the Pectoralis minor migrates cephalo-mesad, leaving its primitive association with the Pectoralis abdominalis and gaining a secondary point of insertion into the medial border and part of the upper surface of the coracoid process, the distal portion of its original tendon remaining as the coraco-humeral ligament between the coracoid process and the humeral capsule. As a reversional ataval variant in Man, and more frequently in the anthromorphs, especially the Chimpanzee, the muscle forms a rounded tendon of insertion which, in part or as a whole, passes outward above the coracoid and under cover of the coraco-acromial ligament to reach the radial tuberosity of the humerus through fusion with the shoulder capsule, at times partly united with the supraspinatus tendon.

This variation is shown in plate IX.

In the case of the M. sterno-scapularis shown in plate VIII the same individual presents another type of this variant in which the caudal part of the Pectoralis minor has the normal coracoid insertion, while the cranial portion develops a tendon which passes over the coracoid process to reach its insertion in the scapulo-humeral capsule.

2. *Variations of the Peroneal Muscles. Extensor quinti digiti brevis.*

The Peroneal group of muscles are to be regarded on comparative anatomical grounds as derivatives from the primitive extensor mass of the toes, modified in the service of the movements of the foot at the ankle-joint.

In the Monotremes the nearest approach to the original condition among extant forms is encountered.

In *Platypus* the lateral group of muscles is composed of the *Peroneus longus*, an early anlage of the *Peroneus brevis* and the *Extensor brevis digitorum*, all three arising from the fibula. The tendons of all three descend on the *ventral* aspect of the ankle to the foot.

1. The *Peroneus longus* inserts on the lateral surface of the cuboid and the base of the 5th metatarsal. A continuation of its tendon, surrounded by an indistinct sheath, crosses the plantar surface of the foot from the lateral to the mesal border to insert into the plantar aspect of the 1st metatarsal. This represents the earliest stage among extant mammalia of the characteristic oblique plantar course of the tendon of this muscle, in which it has not yet given up its primitive lateral insertion into cuboid and 5th metatarsal and its new extension to the mesal border has not yet acquired the freedom and independence of the structure familiar in Man.

2. The *Extensor brevis digitorum* passes to the four inner toes. Its lateral portion separates incompletely from the remainder as

3. the *Peroneus brevis*. This muscle arises in common with the preceding from the proximal portion of the lateral fibular surface, under cover of the *Peroneus longus*, and might well be designated as the *Extensor digiti quinti brevis*. Its tendon descends over the ventral aspect of the distal epiphysis of the fibula and extends to the terminal phalanx of the 5th toe. Near the middle of its course over the 5th metatarsal the tendon sends off a lateral branch which inserts into the lateral surface of the head of the 5th metatarsal and base of its 1st phalanx. This lateral portion of the *Extensor digiti V. brevis* forms the primitive anlage of the *Peroneus brevis* of the higher forms in which it gains greater individuality and independence. Its tendon shifts the primitive distal insertion proximad to the base of the 5th metatarsal and at the same time the muscle separates as a well defined integer from the remaining medial portion of the *Extensor digiti V. brevis*.

The change from this primitive condition, retained in the *Monotremes*, to that encountered in the placental mammals, and particularly in Man, involves the following fundamental modifications:

1. The medial portion of the *Extensor brevis digitorum* supplying the four medial toes, shifts its primitive origin from the fibula caudad, occupying a secondary attachment to the dorsum of the foot.

2. The *Peroneus brevis* separates more completely from the *Extensor digiti V. brevis*, as whose lateral derivative it originally arose, increases in volume and appears as an independent muscle.

3. With the development of the external malleolus the tendons of both the *Peroneus longus* and *brevis* become lodged *behind* that process.

Already in the Marsupalia the *Peroneus brevis* has separated from the *Extensor brevis* and its tendon passes behind the malleolus.

4. The medial portion of the primitive *Extensor digiti quinti brevis*, from whose lateral part the *Peroneus brevis* originally differentiated, may follow the *Peroneus brevis* in part or in its entirety, forming a forward extension of its tendon to the little toe (cf. plate x), or it may be retained as a short extensor of the little toe, arising from the fibula, in close association with the *Extensor longus*. In the lower Primates it thus appears widely distributed in the Prosimiae, as the *Peroneus quinti digiti*, a small muscle, arising from the fibula, whose long and slender tendon descends in company with the tendon of the *Peroneus brevis* and is inserted on the lateral side of the long extensor tendon to the 5th toe.

It is thus found in *Lemur catta*, *L. varius*, *L. nigrifrons*, *Galago crassicaudatus*, *G. garnettii*, *G. allenii*, *Nycticebus tardigradus*, *Tarsius spectrum*, *Cheiromys madagascariensis*.

5. The extensive occurrence of this muscle in the lower primates has led to the differentiation of a muscle peculiar to man and principally responsible for his ability to raise and evert the lateral border of the foot which makes the upright posture and walk possible, while the failure of such differentiation is largely the cause why the anthropoid apes have been handicapped in following the same evolutionary path. This muscle is the human *Peroneus tertius*, which appears as a derivative of the long *Extensor* with insertion into the base of the 5th metatarsal, but occasionally betrays its primitive origin by contributing the short extensor tendon to the lateral toes.

Some of these variants of the peroneal group are remarkably well presented in right foot of the individual shown in plate x.

The Peroneus brevis before reaching its insertion into the base of the 5th metatarsal gives off a well developed tendon which passes to the terminal phalanx of the little toe laterad to its tendon from the long extensor. This in a large measure repeats the primitive condition of *Platypus* in which the Peroneus brevis is derived from a lateral element of the Extensor digiti V. brevis. The medial portion of this muscle appears as the human Peroneus tertius, associated in this instance with the Extensor quarti digiti brevis which has retained its primitive fibular origin and whose tendon in its passage to the 4th toe has contracted an intermediate connection to the base of the 5th metatarsal in close proximity to the insertion of the Peroneus tertius. The medial portion of the Extensor digitorum brevis has moved in the usual manner to the dorsum of the foot, supplying the three inner toes, the great toe receiving in addition to the typical Extensor hallucis brevis the tendon of an accessory element.

A similar variation also is recorded among the anthropomorphic Primates (Orang). It forms a very significant example of a structure normally present in the lower Primates (Prosimiae) reappearing in man and the higher members of the order as a reversional phyletic variant of the ataval value.

B. PROGRESSIVE PHYLOGENETIC VARIANTS.

Two examples may be taken as illustrating evolutionary processes at present active in human organization and looking toward their distant future inclusion in the normal structure of the body.

1. *Variation in the vertebral level of the pelvic girdle. Pelvic advance and retardation.* The normal adult praesacral portion of the vertebral column contains 7 cervical, 12 thoracic and 5 lumbar vertebrae, making a total of 24 praesacral and constituting the 25th vertebra normally the 1st sacral element.

On phylogenetic evidence the conclusion is justified that in Man and the higher Primates a shortening of the longitudinal body axis has taken place in the course of evolution. As one of the results of this process the present average vertebro-pelvic level has been acquired, both regressive and progressive variations occurring at the lumbo-sacral junction.

In general the phylogenetic evidence goes to show that the

level of the attachment of the primitive pelvic girdle to the vertebral column was placed further caudad than at present and that the trunk was originally longer. The acquisition of the bipedal upright posture, completely assumed by man and incompletely attained by the anthropomorpha, led to a progressive shortening of the vertical body measure by the shift of the pelvic arch craniad upon the vertebral line. At any stage in this process the vertebra forming the first sacral element is of course the last to be included within the domain of the advancing pelvis and to become incorporated in the sacrum. Hence the synostosis of the sacral segments takes place caudo-craniad. In man the first sacral vertebra frequently retains traces of its original independence and its fusion with the second sacral is less complete than that obtaining between the remaining segments.

While in the course of this phylogenetic development new elements are added anteriorly to the sacrum from the lumbar column, detachment of vertebrae, which were formerly sacral and which have been passed by the pelvic advance, takes place posteriorly, these being transferred to the caudal or coccygeal series. This is the process defined as *pelvic migration craniad*, or *advance of the pelvic arch* on the vertebral column. It normally terminates in its present stage in man when the 25th segment becomes incorporated in the sacrum as the first sacral vertebra.

The pelvic advance upon one or both sides may be carried forward beyond the present average level. This is *increase* or *advance of pelvic migration* and constitutes a variation of *progressive* significance, in which the individual anticipates the progress of the evolutionary shift of the girdle craniad, carrying it beyond the point as yet attained by the majority of the race. The number of the praesacral vertebrae is then reduced to 23. (Fig. 17.)

Plate XI shows three stages in this process. In all three instances there is the normal number of seven cervical and twelve thoracic vertebrae, the 20th total vertebra becoming the 1st lumbar.

The individual shown in figure 1 of plate XI represents the lowest degree of pelvic advance, the costal processes of the 24th vertebra exhibiting a tendency toward sacralization, which on the

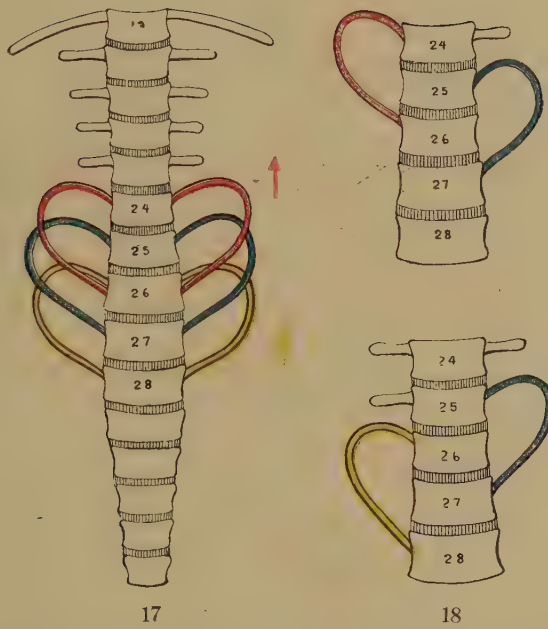


Figure 17. Schema of pelvic migration in Man. Blue: Normal level of vertebro-pelvic attachment. Red: Pelvic advance. Yellow: Pelvic retarding.
 Figure 18. Schema of Lumbo-sacral transitional vertebra.

left side has attained a point of iliac contact. In figure 2, with marked reduction of the 12th rib, the 24th vertebra is a typical lumbo-sacral transitional segment, lumbar on the right, completely sacral on the left side.

In figure 3, the 24th vertebra is symmetrically sacralized on both sides. The praesacral column has been reduced to 23 segments, of which the 4 caudal elements are lumbar. The pelvis has traveled cephalad one segment beyond the present average normal pelvico-vertebral level and the individual furnishes an instance of a complete progressive phyletic variation.

Conversely the pelvic migration may in individual instances be arrested, again on one or on both sides, at the level of the 26th total vertebra. This is *retardation of the pelvic advance* one segment behind the level normally attained by the average individual, and constitutes a variant of *regressive* significance. The number of the praesacral vertebrae is then increased to 25. (Fig. 17.)

Plate XII shows three instances in which this condition exists in varying degrees. In all three again there are seven cervical and twelve rib-bearing vertebrae.

In figure 1, the 25th vertebra is transitional, completely sacralized on the left side, while its right costal process has not attained iliac contact, and approaches the lumbar type.

In figure 2, the 25th vertebra has not entered into the sacral complex, the line of separation involving both the centre and the lateral masses. The costal processes are reduced on both sides and attain only incomplete iliac contact.

In figure 3, the 25th vertebra is typically lumbar in character on the left side. The right costal process is broadened, but only reaches the ilium at one restricted point. The 26th segment constitutes the 1st sacral vertebra, there being 25 praesacral elements, of which the caudal 6 form the lumbar series.

If either the variant of increase or retardation develops only on one side, it results in the formation of a *lumbo-sacral transitional vertebra*, in which one half of the bone shows sacral, the opposite half lumbar characters. (Fig. 18.)

The normal pelvic attachment involves the 25th, 26th and 27th vertebra, and is indicated in the blue color. If either advance

(red) or retardation (yellow) of pelvic advance occurs on one side only, a lumbo-sacral transitional vertebra develops with resulting pelvic asymmetry.

The two examples given on plate XIII show the frequent type of the low grade of the variation. In figure 1, sacralization is complete on the left side, incomplete on the right. In figure 2, the first sacral vertebra is more independent on both sides, and the right costal process enters only to a slight degree into the formation of the lateral mass.

Clinically these cases, occurring in women, become of grave import by leading to a distinct type of oblique pelvic narrowing which may seriously interfere with the successful termination of pregnancy. They also can determine an important group of lateral scoliotic curvatures, which in young subjects can be corrected by surgical means, through the resection of the atypical sacro-iliac point of articulation.

In increased pelvic migration the lumbar column may be reduced to four segments in which case the thoracic column remains normal, with 12 rib-bearing vertebrae. Or the lumbar column may contain five vertebrae, the normal 12th thoracic segment having become the 1st lumbar by synostotic union of its neural arch and rib, thus reducing the number of thoracic rib-bearing vertebrae to eleven. In arrested pelvic shift the lumbar column may contain six vertebrae, with a normal thoracic series of twelve rib-bearing vertebrae, or there may be five lumbar segments, the normal first lumbar having developed the costal process as a moveable thirteenth rib.

The work of Bardeen on human embryos has corrected the earlier view of Rosenberg, and has shown that advance or retardation of pelvic migration does not take place ontogenetically during individual development. The attachment of the skeletal blastema of the ilium to the vertebral column may vary in its level, on one or both sides, in individual embryos, but once formed it does not shift during the process of further development for that particular embryo.

The progressive and regressive variants just considered have therefore the value of *phylogenetic* in contrast to *ontogenetic* varia-

tions. The evolutionary steps by which the present normal level of the pelvic girdle in its relation to the vertebral column has been attained are no longer rehearsed in the ontogeny of the individual. They are, however, clearly outlined by the phyletic variations of both the embryo and the adult.

In the Anthropomorph Primates the same process is to be observed, modified by the intrinsic structural conditions obtaining in these forms. Of the four extant anthropoid apes, three, the Orang, Chimpanzee and Gorilla, have only partially and incompletely attained the upright posture and bipedal progression, the enormously elongated fore limbs serving as important and necessary supports. Yet in all three of these apes pelvic migration cranial and resulting shortening of the long diameter of the body cavity has been carried one segment further than in man. The reason for their failure to reach the human standard must therefore lie in some other detail of their structure. Three facts are here of importance:

1. The foot is still a prehensile organ. The adjustment of the peroneal musculature has not reached the point at which it suffices to elevate the outer margin of the foot and oppose the entire planta to the ground. The ape, in the upright posture, walks largely upon the outer border of the foot. To a great extent this is due to the failure to develop the typically human *Peroneus tertius*, passing between the fibula and the base of the fifth metatarsal bone and strongly everting the foot. (cf. supra plate P. x).

2. The sternum in the anthropoidea is very short, relative to the total body length. The forward sag of the abdominal contents is hence in the upright posture supported in the resulting unduly long pubo-sternal interval solely by the muscular and other soft structures of the ventral abdominal wall. Anyone observing these apes during life will note the degree to which their attempts at upright walking are handicapped by the protrusion of the pendant ventral paunch.

3. The pelvis is incompletely adapted to receive and support the weight of the abdominal viscera transmitted from above in the vertical line. The lower pelvis is deep and narrow, approaching the carnivore, rather than the widened and roomy human type.

In the upper pelvis the plane of the ilium is practically vertical and extends mainly in the dorsal line nearly to the lower rib border, whereas in Man the oblique shelf of the ilial shovel extends well latero-ventrad and affords considerable support to visceral weight transmitted from above.

To counteract these disadvantages, however unsuccessfully, the advance of the pelvic girdle has been carried one segment further craniad than is normal in Man, there being 23 praesacral vertebrae, the 24th forming the first sacral segment.

The Orang has usually 12 rib-bearing vertebrae and 4 free lumbar segments. (Plate xiv, fig. 1.) The Chimpanzee usually has 13 thoracic vertebrae, reducing the lumbar column to 3 free vertebrae. At times this ape has 13 thoracic and 4 lumbar vertebrae, thus shifting the pelvis further caudad than usual, the 25th vertebra, as in Man, becoming the 1st sacral. This is the case in two skeletons of my collection.

The Gorilla has 13 thoracic and 3 free lumbar vertebrae, the 24th segment becoming the 1st sacral. In this animal the 24th vertebra, although it assumes the relationship to the pelvis of the 1st sacral, retains usually its independence, i.e., it does not become fused with the 2nd sacral, as in the Orang and Chimpanzee. This is the case in the two Gorilla skeletons of my collection, both mature adult individuals. (plate xiv, fig. 2). Further the 24th vertebra of the Gorilla tends to present on one or both sides lumbar character, especially of the costal process, although articulating with the ilium. These facts indicate that the forward shift of the pelvis in this animal to the level of the 24th segment is here a more recent phylogenetic acquisition as compared with Orang and Chimpanzee.

The fourth anthropoid ape, *Hylobates*, is very largely arboreal in his mode of life, and hence not affected by the mechanical problems of the upright posture and bipedal progression operative in the case of the remaining three members of the group.

In consequence of this pelvic migration is usually arrested at a more caudal point.

In the various species of the Gibbon there are usually 13-14 rib-bearing vertebrae and 4-5 lumbar segments. This brings the

total number of the praesacral vertebrae to 25, and the 26th becomes the 1st sacral. The forward shift of the pelvis thus stops one segment caudad of the normal in Man, and two segments behind the level usually attained by the three other Anthropoids, Gorilla, Orang and Chimpansee. There is considerable variation in this respect in individual Gibbons. One of my preparations (*Hylobates hoolock*) has 12 thoracic, and 5 lumbar, the 25th total vertebra forming the 1st sacral and conforming to the normal condition in Man. This is an instance of progressive variation in the Gibbon in the sense above defined. In general, therefore, Man, with the 25th total vertebra constituting the 1st sacral, occupies an intermediate position between the three higher Anthropoids, Orang, Chimpansee and Gorilla, where the 24th becomes the 1st sacral, and the Gibbon in which the pelvic shift is arrested further caudad, the 26th total vertebra becoming normally the 1st sacral.

Individual variations in both directions bridge the gap between the typical condition in Man and that obtaining in the Anthropomorpha.

In the lower Primates, in accordance with their more constant quadrupedal position, the lumbar column is longer and forms a uniform ventrally concave curve in prolongation of that of the thoracic segment. The pelvis is located further caudad. Thus, among the Cercopithecidae, *Macacus* has 12 thoracic and 7 lumbar vertebrae, *Cynocephalus* 13 thoracic and 6 lumbar, making in either case the 27th total vertebra the 1st sacral.

Reduction of the lumbar segment is also seen in the lower mammalia in response to specialized functional adaptation, and is accomplished either by forward shift of the pelvis or caudal extension of the rib-bearing group. Thus in the arboreal Sloths the weight of the body contents in the habitual inverted position (plate xv, fig. 1) is carried, as in a basket, by the vertebral column, pelvis and the increased number of the rib arches. In *Choloepus* the thoracic series, with 23 rib-bearing vertebrae, approaches close to the pelvis, leaving only 3 free lumbar segments intervening, and the apparatus serves admirably for the support of the viscera in the inverted suspended position. In this animal the comparison of the immature and adult skeleton is of interest

in respect to the more complete incorporation in the latter of the sacrum, and especially of the 1st sacral element, in the arch of the pelvis. (plate xv, figs. 2, 3).

Migration of the pelvis is also observed in the lower vertebrates.

It is stated that in the fossil amphibian *Branchiosaurus* the comparison of juvenile and adult specimens shows a shifting of the pelvic arch along six to seven vertebrae.

A summary of the problem of pelvic migration offers the following considerations:

1. The reduction of the vertical diameter of the body cavity develops phylogenetically.

2. The incentive is given in bipedal Primates in which the weight of the abdominal viscera thrusts forward as well as downward, by the mechanical advantage gained in reducing the length of the unsupported ventral body wall in the pubo-sternal interval.

3. The increased forward shift of the pelvis beyond the level normal in Man seen in the semi-bipedal anthropomorphs, Orang, Gorilla and Chimpanzee, is to be interpreted as an attempt to make up in this way for the other structural conditions unfavorable to the assumption of the upright posture, viz.

- a. The relative shortness of the ventral thoracic wall, thus increasing the pubo-sternal interval.

- b. Failure to adapt the foot to upright walking by development of the everting muscle, the *Peroneus tertius*, which elevates the lateral border of the foot.

- c. Inadequacy of visceral support by the pelvis, especially by the lateral expansion of the ilium.

4. The direction of the shift is shown by the caudo-cranial progress of the sacral synostosis.

5. Phylogenetically correlated reduction of the functional ribs and raising of the caudal pleural limits.

As the pelvis advances cranial on the vertebral column the distal thoracic vertebrae tend to reduce or lose their free costal elements and to become assimilated to the lumbar column. This is shown by

a. The ontogenetic loss of the free 13th rib which becomes incorporated in the first lumbar as its transverse process, according to the results of Rosenberg, which are, however, questioned by Bardeen.

b. The occasional default of the 12th rib, making the formula Th. 12 L 6.

c. The reduction of the 11th and 12th costo-transverse articulations and the fact that the 11th costo-transverse joint, although laid down in the embryo, is lost during subsequent development.

d. Reduction and great variability in the development of the 11 h (15-28 cm.) and 12th (2-27 cm.) ribs.

6. Variations, both total and divisional, in the number of vertebral segments.

7. The occurrence of lumbo-sacral transitional vertebrae.

8. Phylogenetic evidence of the pelvic shift in other Primates and in lower vertebrates, and variations in the same.

Table of vertebral formula of man and lower primates with variations

	MEN					CHIM- PANSEE		GORILLA		ORANG	GIBBON		MACACUS	CYNOCEPH- ALUS
	Normal	Variation within normal total number		Arrest of pelvic shift	Advance of pelvic shift	Normal	Variant	Normal	Variant	Normal	Normal	Variant	Normal	Normal
Cervical.....	7	7	7	7	7	7	7	7	7	7	7	7	7	7
Thoracic.....	12	11	13	12(13)	12(11)	13	13	13	13	12	13-14	12	12	13
Lumbar.....	5	6	4	6(5)	4(5)	3	4	3	4	4	5-4	5	7	6
Number of praesacral vertebrae..	24	24	24	25	23	23	24	23	24	23	25	24	26	26
First sacral..	25th	25th	25th	26th	24th	24th	25th	24th	25th	24th	26th	25th	27th	27th

2. A second example of the phylogenetic progressive variation occurring in Man may be found in the congenital absence of the Vermiform Appendix of the Caecum. In these cases the caecal outgrowth from the embryonic intestine only develops to a degree sufficient for the establishment of an adult pouch of the normal dimensions. The distal portion of the embryonic sac, ordinarily furnishing the appendix, defaults. Considering the evident vestig-

ial character of the caecal appendix, instances of its congenital absence may well be interpreted in our sense as progressive variation looking toward the eventual attainment of the evolutionary stage in which the human large intestine no longer carries normally this menacing reminder of its phyletic past.

* At the present level of human evolution the variation is exceptional.

There are recorded in the literature some thirty instances. Some of these, based on findings during operation, may be considered doubtful. But, discarding all questionable cases and those incompletely described in the older literature, there remain some ten instances of true congenital absence of appendix. Two of these have come under my personal observation and I can vouch for them as genuine examples of the variation. They are shown in plates xvi and xvii reproduced here from my "Anatomy of the Peritoneum" through the courtesy of the publishers, Messrs. Lea and Febiger. In both cases careful examination of both the serous and mucous surfaces of the caecum demonstrated the entire absence of the appendix. The subjects from which they were obtained presented no scars or other evidences of operative removal. The peritoneal environment was clean, without trace of previous inflammatory or other pathological processes. They are both, therefore, authentic instances of complete congenital absence of the appendix, not of so-called 'retroperitoneal' or 'hidden' appendix.

The two examples differ from each other in some details. In the case shown in plate xvi the caecum is rounded and globular. The ventral longitudinal muscular band descends vertically and is continued to the lowest point of the pouch, which greatly resembles the caecum of a typical cynomorphous monkey.

In the second case (plate xvii) the caecum turns upward and to the left, terminating in a sharp point to which, on the serous surface, several lobules of epiploic fat are attached.

The foregoing classification of variation finally serves as a basis for the general consideration of the evolutionary theories. These are treated largely from the historical standpoint, with somewhat detailed consideration of the Roux-Weismann theory

and of the chromosomal basis of inheritance and evolution. Special stress is laid on the distinction between the general aspect of evolution and Natural Selection or "Darwinism" in the narrower sense, and between continuous and discontinuous variation. The problem of the evolutionary aspect of Mutation is discussed, for the Mammalia, on the hand of phylogeny of the mammalian lung, with the fundamental architectonics of the organ in the Hystricomorphs and Mustelidae as a basis. This subject will be presented to the Association at a later period of the present meeting.

The topics presented in the foregoing outline are covered on the average in about seven lectures. I do not find this an excessive proportion of the time assigned to Anatomy in the general course, in view of the educational value which, in my judgment, belongs to the subject, and in consideration of the fact that many of the conditions here treated fall within the province of the regular anatomical instruction. They are merely displaced to some extent in the systematic order of their presentation and assembled for the purpose of more generalized interpretation.

The student is referred for collateral reading and study to the following works:

Conklin, E. G., 1917. Heredity and Environment.

Morgan, T. H., 1916. A Critique of the Theory of Evolution.

Lock, R. H., 1911. Variation, Heredity and Evolution.

Osborn, H. F., 1892. Present Problems in Evolution and Heredity, Cartwright Lectures.

Wilson, E. B., 1900. The Cell in Development and Inheritance.

PLATE I

EXPLANATION OF FIGURES

1. Human adult, costocoracoid ligament and membrane. The fibres of the underlying Subclavius muscle show through the cut in the membrane.
2. Adult human, Coracoid insertion of the Subclavius.

CLAVICULAR
PECTORALIS MAJOR.

COSTO-CORACOID
LIGAMENT AND MEMBRANE.

DELTOID.

PECT. MAJOR.

BICEPS.

CORACO-BRACHIALIS.

PECTORALIS MINOR.

1

COSTO-CLAVICULAR LIG.

SUBCLAVIUS.

CORACO-CLAVICULAR LIGS.

CORACO-SCAPULAR
INSERTION OF
SUBCLAVIUS.

BICEPS
AND
CORACO-BRACHIALIS.

PECTORALIS MINOR.

SUPERIOR TRANSVERSE
SCAPULAR LIG.

2

PLATE II

EXPLANATION OF FIGURES

1. Right and left humeri in a specimen of *Hyaena striata*, showing the occurrence of the entepicondylar foramen as a reduced variant on the right side.
2. Left humerus of *Felis leo*, showing entepicondylar foramen characteristic of the Felidae.
3. Series of adult human humeri with supracondylar process.

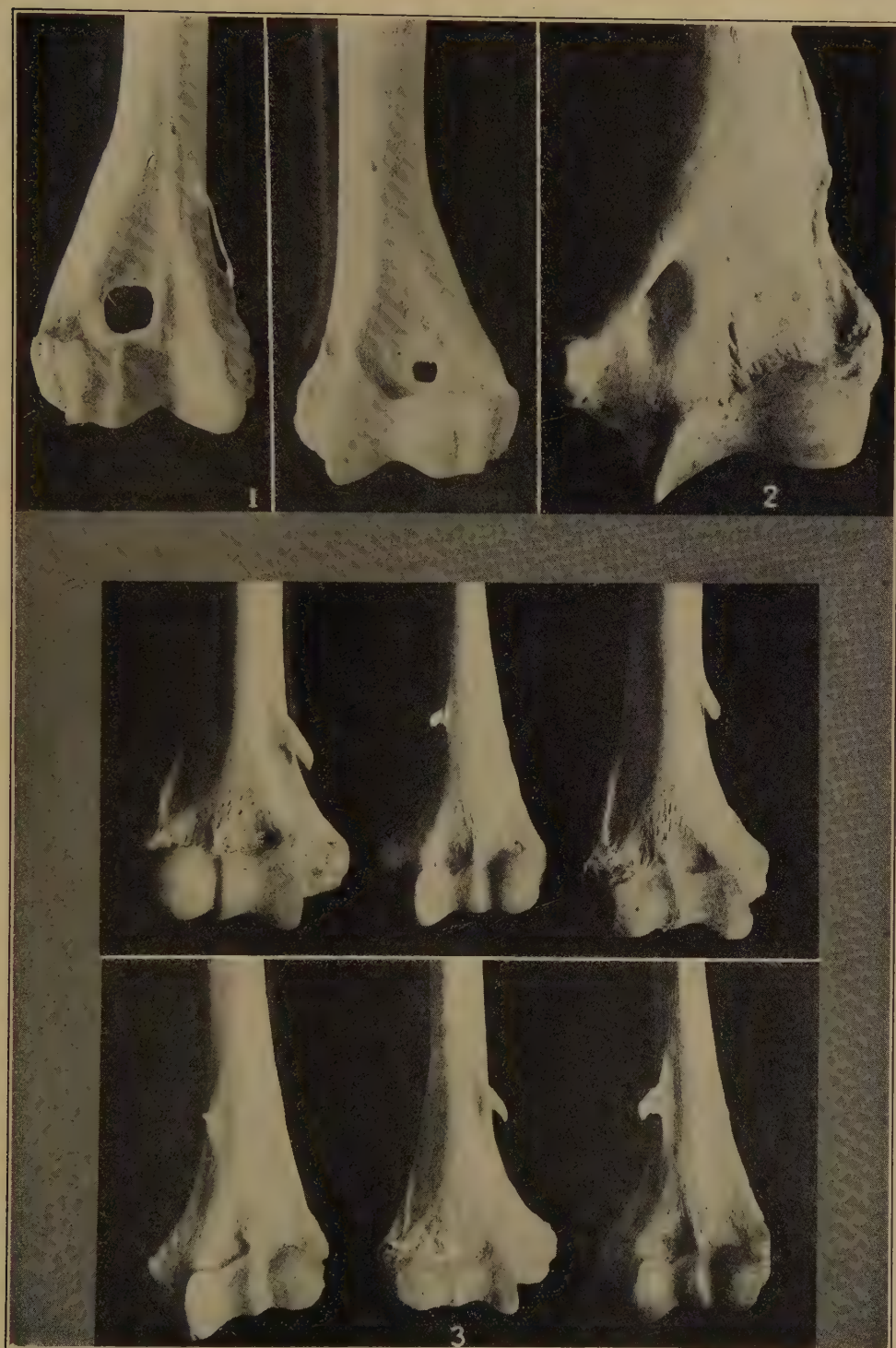


PLATE III

EXPLANATION OF FIGURES

Comparative series of left mammalian humeri illustrating the occurrence of the entepicondylar foramen.

1. *Platypus anatinus*, Monotreme carrying entepicondylar foramen.
2. *Didelphis marsupialis*, Marsupial carrying entepicondylar foramen.
3. *Tatusia novemcincta*, Edentate carrying entepicondylar foramen.
4. *Talpa europea*, Insectivore carrying entepicondylar foramen.
5. *Erinaceus europeus*, Insectivore lacking entepicondylar foramen.



PLATE IV

EXPLANATION OF FIGURES

Comparative series of left mammalian humeri illustrating the occurrence of the entepicondylar foramen.

1. *Canis vulpes*, Cynoid carnivore lacking entepicondylar foramen.
2. *Paradoxurus typus*, Aeluroid carnivore carrying entepicondylar foramen.
3. *Mustela pennanti*, Aeluroid carnivore carrying entepicondylar foramen.
4. *Nasua rufa*, Aeluroid carnivore carrying entepicondylar foramen.
5. *Lemur xanthomystax*, Prosimian carrying entepicondylar foramen.
6. *Otolicnus crassicaudatus*, Prosimian carrying entepicondylar foramen.
7. *Lagothrix humboldtii*, Platyrrhine monkey carrying entepicondylar foramen.
8. *Ateles* sp? Platyrrhine monkey carrying entepicondylar foramen.
9. *Ateles ater*, Platyrrhine monkey carrying entepicondylar foramen.
10. *Cebus capucinus*, Platyrrhine monkey carrying entepicondylar foramen.
11. *Macacus rhesus*, Catarrhine monkey lacking entepicondylar foramen.



PLATE V

Adult human, Supracondylar Process and associated structures.

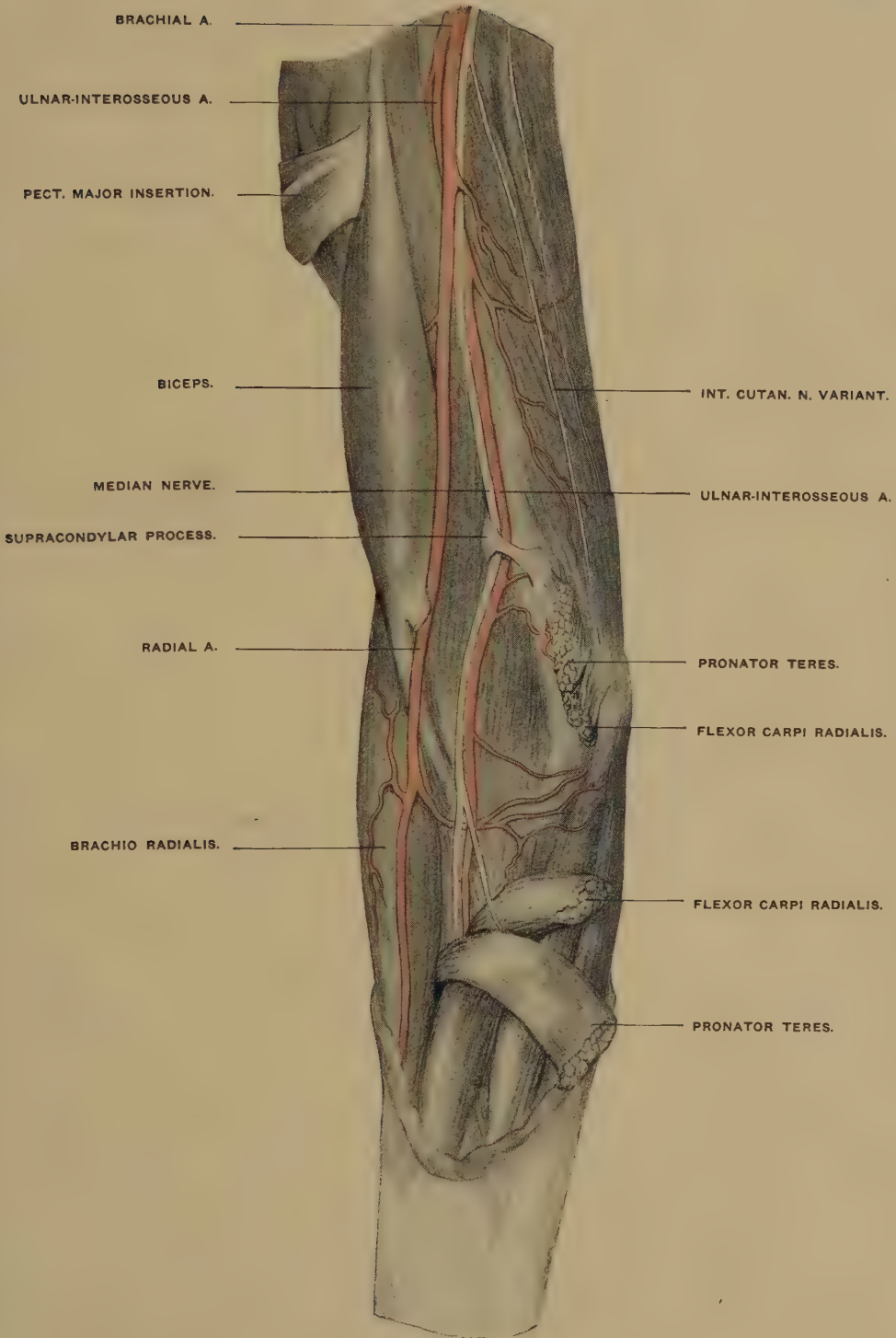


PLATE VI

Human adult, *M. Omo-cleido-transversarius*.

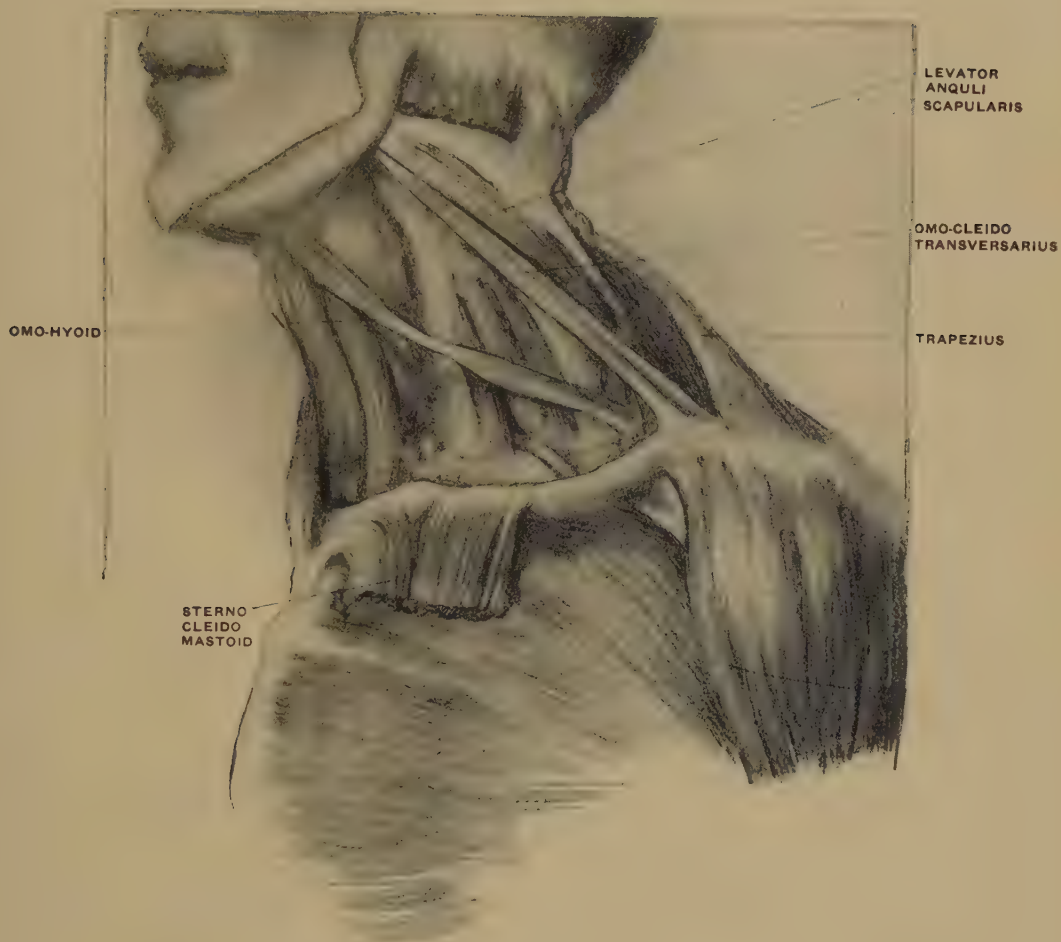


PLATE VII

EXPLANATION OF FIGURES

1. M. Omo-cleido-transversarius in *Ateles ater*.
2. M. Sterno-costo-scapularis in the same form.



PLATE VIII

Adult human, M. Sterno-costo-scapularis.

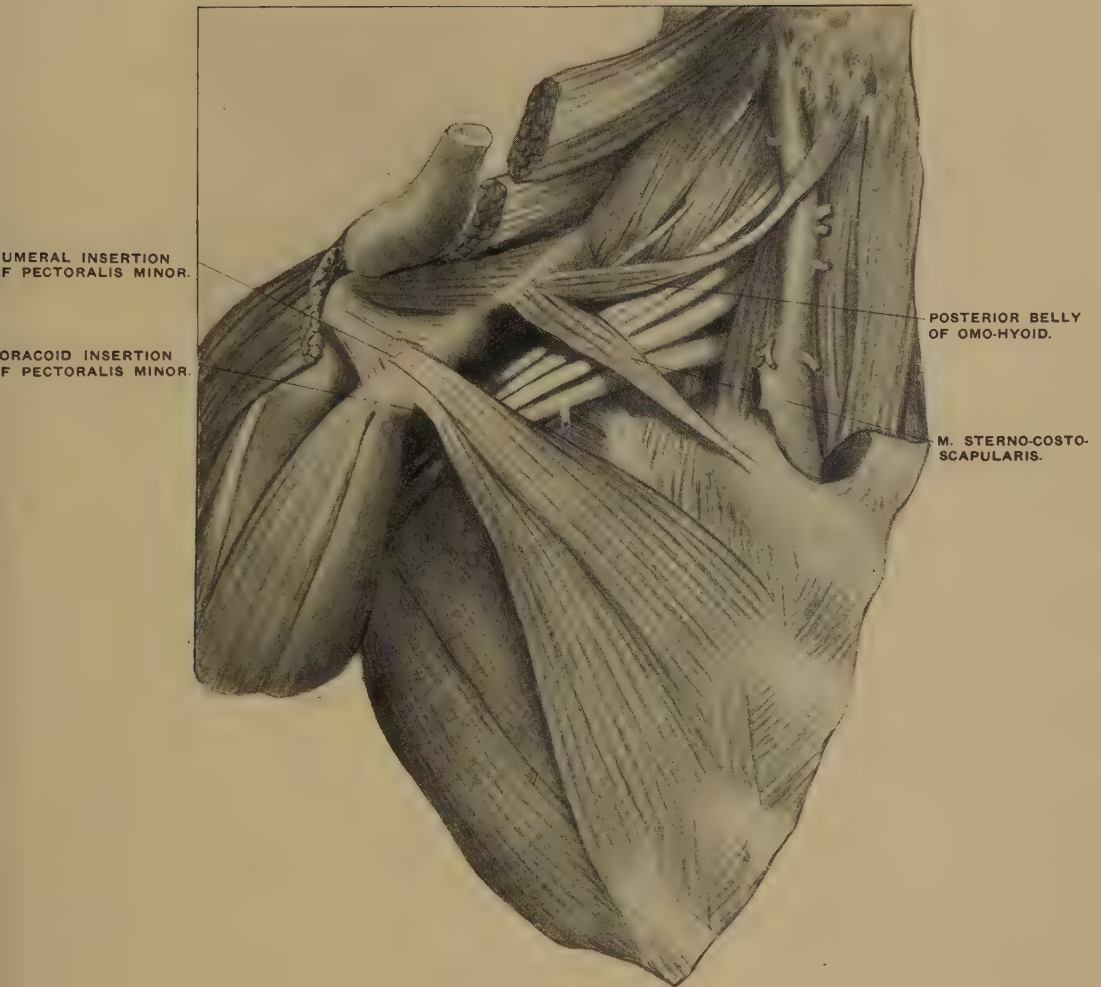


PLATE IX

Adult, human, humeral insertion of the Pectoralis minor.

CORACO-ACROMIAL
LIG., DIVIDED.

HUMERAL INSERTION
OF PECT. MINOR.

SUBCLAVIUS.

PECT
MAJOR

CORACO-
BRACHIALIS.

BICEPS.

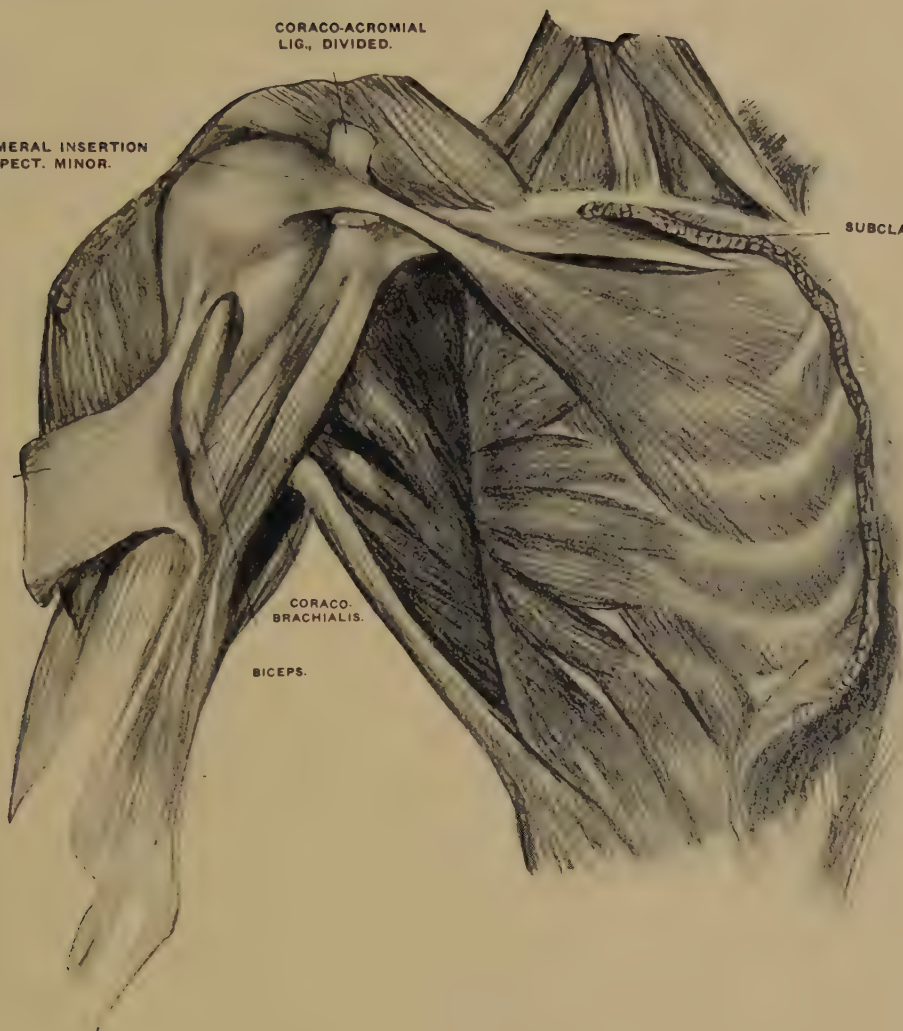


PLATE X

Adult human, variations of the Peroneal musculature.

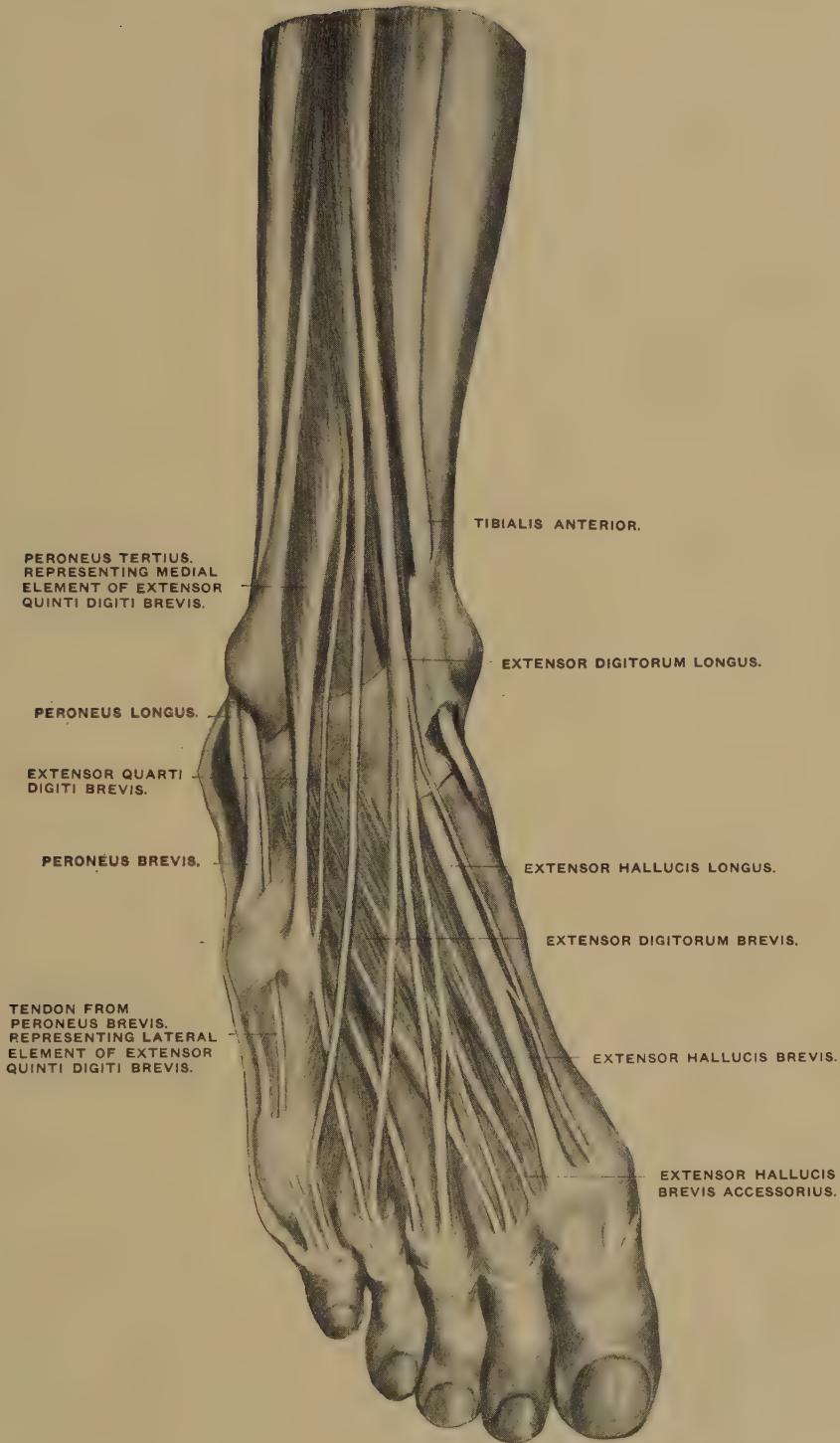


PLATE XI

Adult human instances of phyletic advance of pelvic migration.

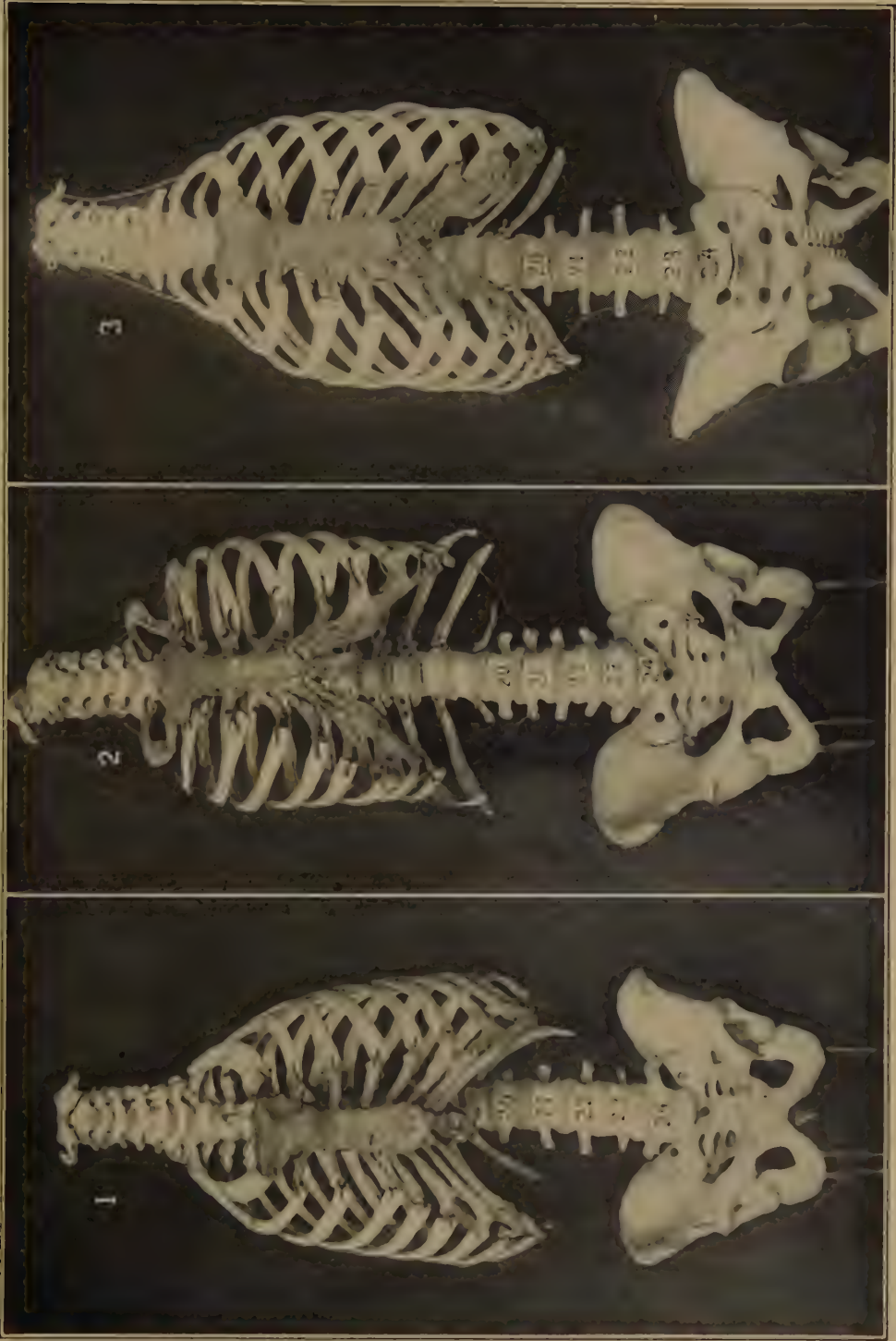


PLATE XII

Adult human instances of phyletic retardation of pelvic migration.

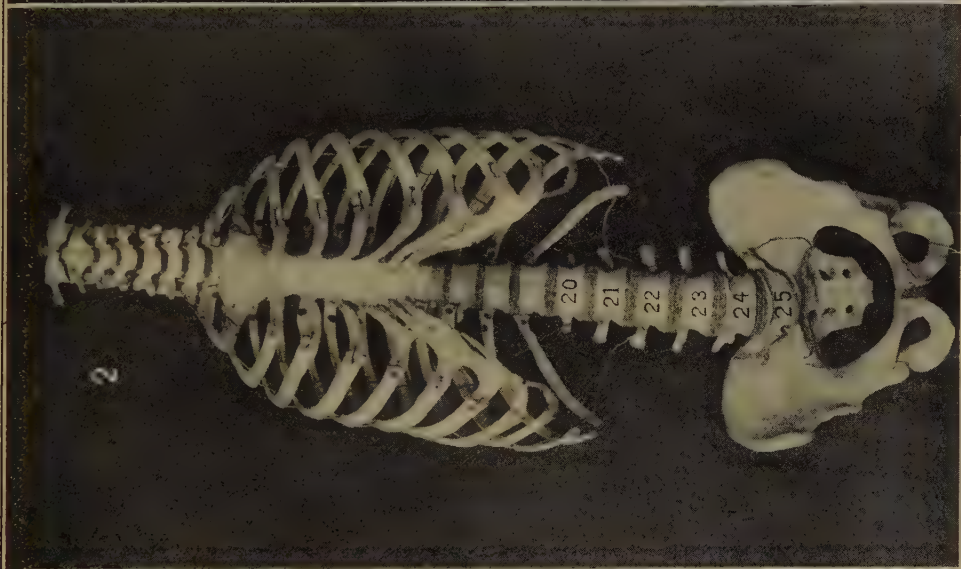
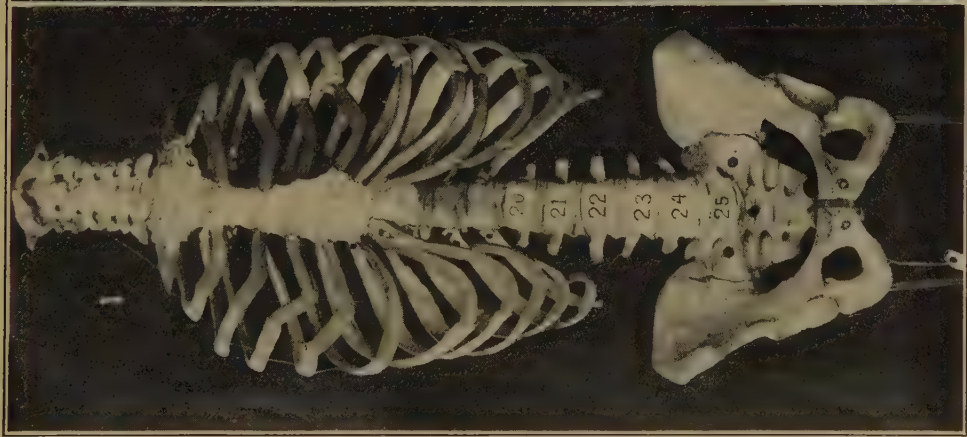


PLATE XIII

Two adult human sacra with slighter degrees of Lumbo-sacral transitional variation.

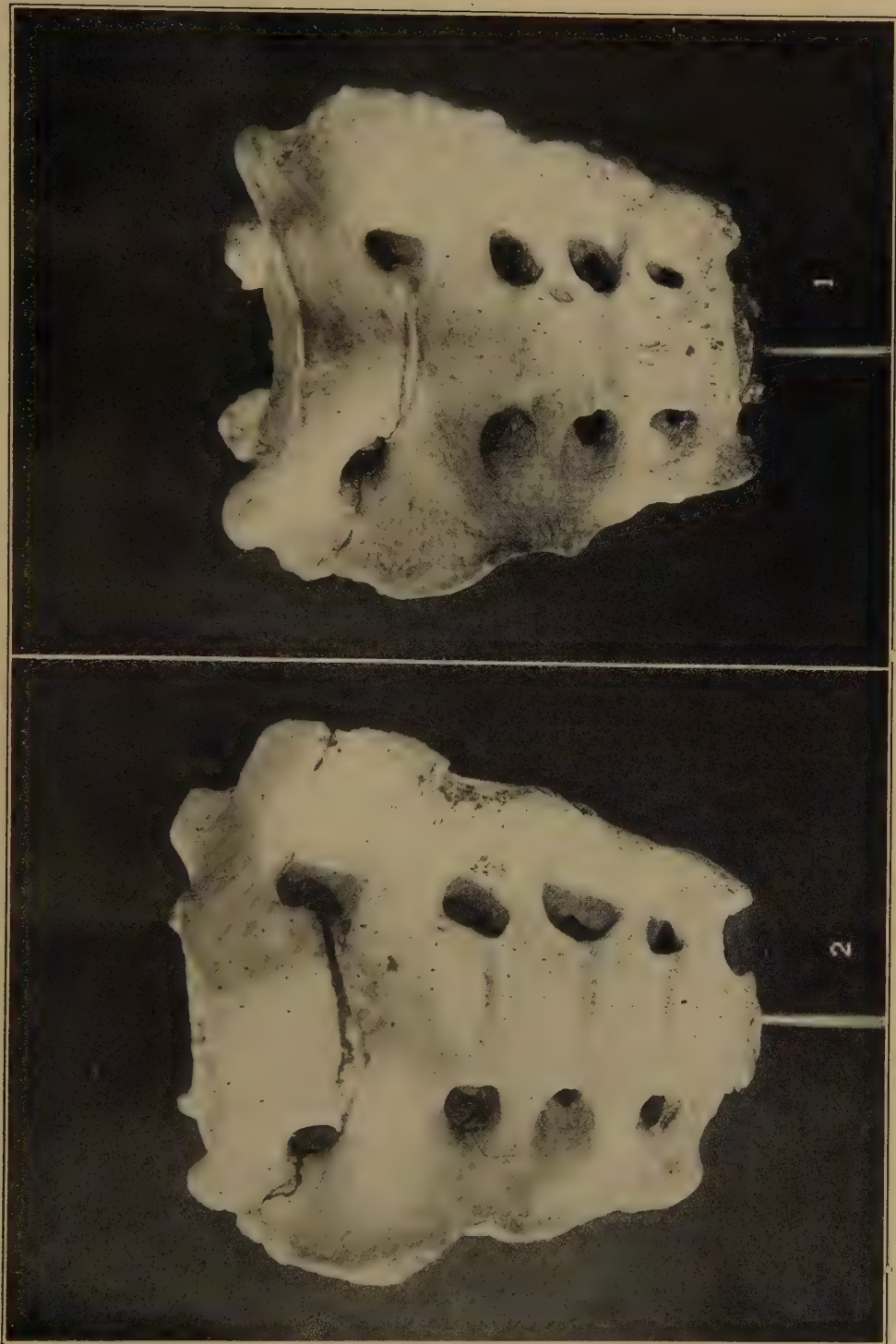


PLATE XIV

1. Skeleton of *Simia satyrus*, the *Orang*.
2. Skeleton of *Gorilla savagei*, the *Gorilla*

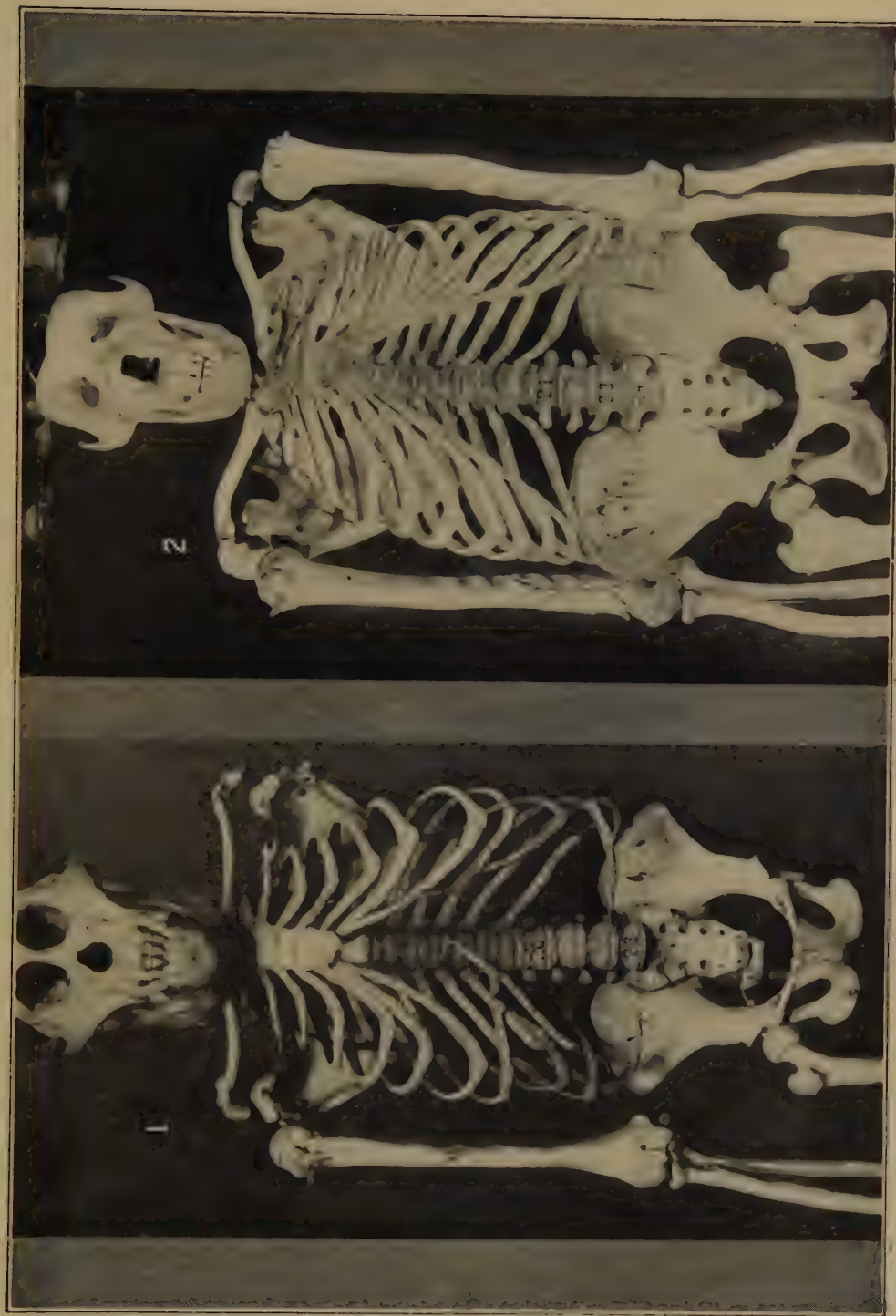
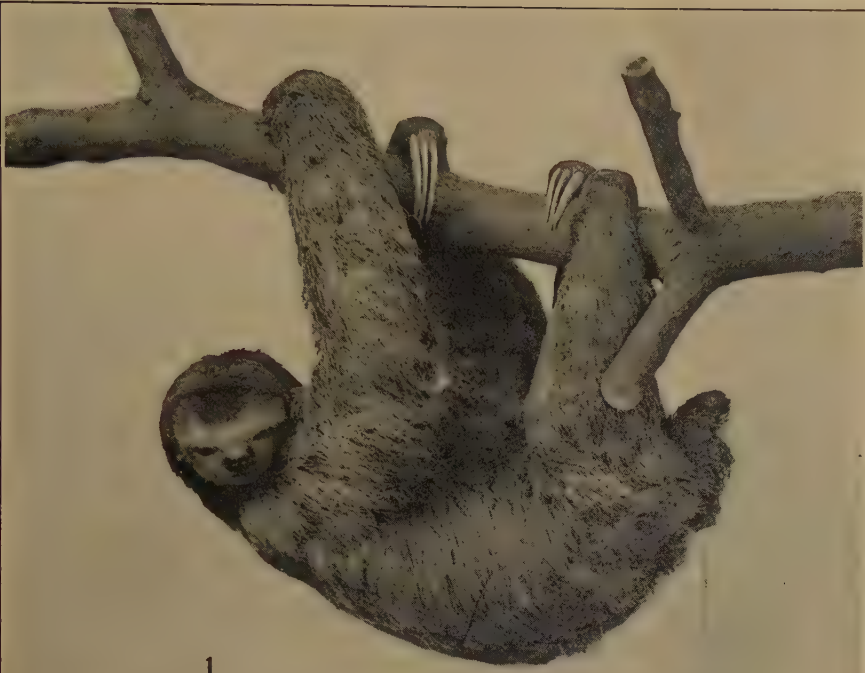


PLATE XV

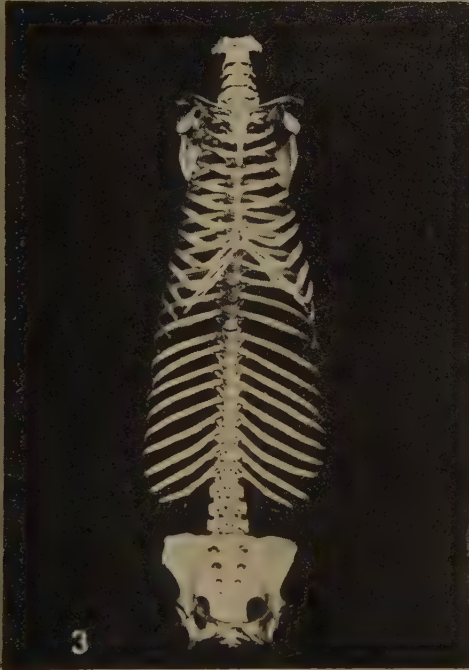
1. Habitual position in life of *Bradypus tridactylus*, the three-toed Sloth.
2. Axial skeleton of young specimen of *Choloepus didactylus*, the two-toed Sloth.
3. The same of an adult individual.



1



2



3

PLATE XVI

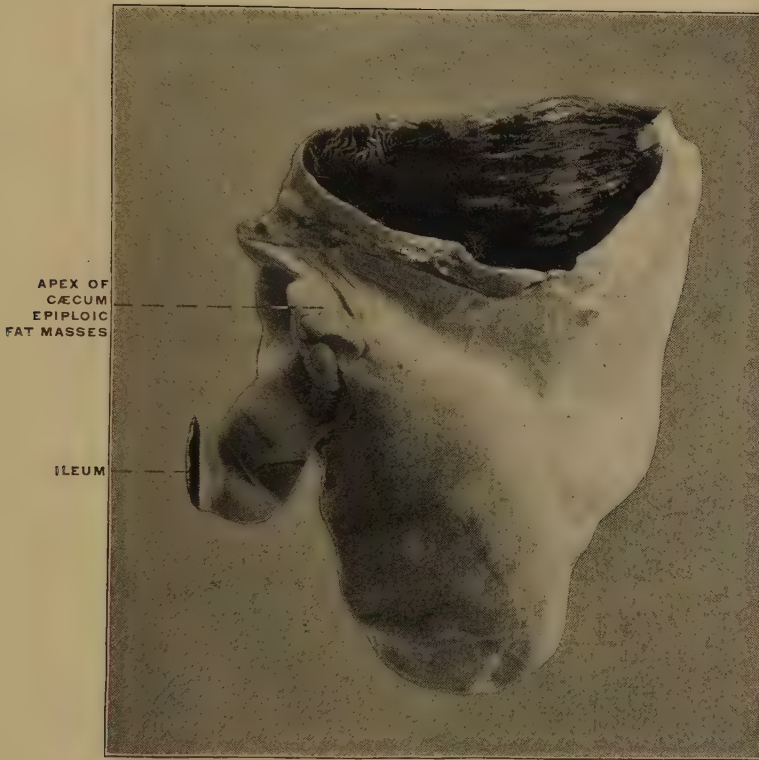
Congenital absence of the Vermiform Appendix in Man.



DORSAL VAS-
CULAR FOLD
AND EPI-
PLOIC FAT

PLATE XVII

Congenital absence of the Vermiform Appendix in Man.



DISCUSSION

PROFESSOR SCHULTE:

In opening the discussion of Professor Pohlman's direct and sensible paper, I would call attention to what indeed seems to me implicit in this paper, namely, the relativity of any course in gross anatomy. The best course in any circumstances is the one which best utilizes the personal ability and resources of the instructor, the material means at hand, and best stimulates and develops the particular group of students taking it. It should be interesting—the subject is; the memorization of details is not. It is necessary to vitalize the facts of anatomy. To do this we must bring the facts into relation with some biologic process, and here we have at least three at hand. The ontogenetic and the phyletic and the physiologic. Of these I would urge the claims of the last as a means of increasing scientific interest in the study and teaching of gross anatomy. Embryology has an assured place in the medical curriculum and comparative anatomy is in no need of defenders. In emphasizing the use of function as means of elucidating structure, I am harking back to a very old and very sound tradition and one which I believe is peculiarly suitable to the practical temper of our nation and the times in which we live. It has a direct bearing upon the prospective activities of the majority of our students, and they like ourselves are prone to be interested and diligent in matters bearing upon their personal problems. I believe that there is wisdom in following the path of least resistance, and I am confident that in pursuing the study of structure and function jointly we are not alone following a useful tradition of our science, but also are inducing our students into methods of thought that tend to inculcate a scientific habit of mind and stimulate inquiry.

° PROFESSOR STOCKARD:

It is particularly interesting to note that each of the speakers has dealt with the important principles of teaching anatomy, and not with the trivial details involved in the kind of instruments or apparatus to be used. This, in itself, is a most encouraging indication of the general attitude of the Association.

One of the speakers, however, has intimated that anatomists may be divided into two classes—investigators and teachers—and that good investigators may be rather poor teachers and vice versa. Everyone must admit that good investigators are not always good teachers, but it is questionable to my mind whether one who is not an investigator is ever a really good teacher. The two things, teaching and investigation, should go hand in hand, and in my own personal experience the best teachers I have ever known and those who have been most stimulating to their students have also been most eminent scientific investigators. The investigator is stimulated by lively contact with bright and inquisitive students and the student admires and feels it a privilege to be taught by a person who has contributed to the knowledge of the subject. While, on the other hand, the pedantic display of memory feats and the juggling of the details of a subject on the part of a teacher rarely ever impresses the serious student.

It is the first duty of a teacher to present his subject in a simple and easy manner so that a beginner or a layman can understand it. Few things are so intricate that they cannot be discussed simply and clearly during all parts of a course. It is self-evident that a person inclined to present his subject in a complex manner, making it difficult to understand, is a failure as a teacher and will rarely succeed in obtaining an attitude of interest from even the most capable students.

It has been particularly instructive to hear Professor Bardeen's discussion of the uses he makes of x-ray plates and living models. We have found the same material particularly useful at Cornell in a slightly different way.

The appearance of the living human body is a familiar object to all beginning medical students. They have a more or less selfish interest in the human body, and therefore it becomes splendid

material with which to excite the most active curiosity and desire for study and investigation if properly held out. The most evident thing on the body is the skin, yet the beginner knows almost nothing about it. So we begin our course the first day with a nude model and consider the simple things of general interest about the skin. For example, it is pointed out in a non-technical manner that its most important function is to maintain and contain the individuality of the body, just as the ectoplasmic surface contains the amoeba. When the skin is broken or destroyed, the body fluids leak out and the surrounding medium gets in, and if a very extensive area of skin has been lost, the body cannot maintain itself without this cover and the individual begins to go to pieces. The skin, after all, is a wall which contains the man. The wall has many other still important functions to perform, such as regulating the body temperature—excretion, secretion, etc.; these functions are all discussed from a structural standpoint. Finally, the skin is seen as an enormous sense organ through which we learn much by the sense of touch. All the other organs of special sense—the retina, ear, nose, and taste-buds—are shown to be derived from the skin layer, and actually the central nervous system may be broadly considered as modified skin.

Such introductory points fascinate and interest the student and he dissects the skin and all other parts with a livelier interest, and it becomes the duty of the instructor to stimulate his imagination with suggestive questions and to control his observations until they become accurate. The exceptional student soon begins to feel himself on firm ground and to correlate his observations, and then gradually to indulge in that most valuable mental process—constructive imagination. The most accurate observer is the most likely to properly build up or construct in his mind the complex mechanisms by which the bodily functions are performed. All must depend upon accurate observation, since only on this can proper deductions be based.

Certainly, there is nothing more important that a physician or an anatomist will have to do than to make careful and correct observations on the materials which he studies, and from such

observations he must construct with carefully trained imagination an interpretation of the problems concerned.

Our present school and college systems, unfortunately, do much to crush and discourage the instinctive powers of observation and curiosity shown by most normal children. It is remarkable how well the average untrained young child observes and also how curious he is to understand what he observes. The uneducated person living in the country and woods where these powers are useful continues to develop them. But the present college graduate, so far as his behavior in the laboratory goes, shows almost no indication of the remains of that childish instinct to observe the things around him. It becomes the duty of the anatomical department to try and revive or fan into life this crushed instinct to observe, and we have found the use of living models an excellent means of stimulating keener interest and more careful observation during the dissection of the cadaver.

PROFESSOR DANFORTH:

Dr. Terry, prevented from being present at this meeting, asked me to say just a word about the treatment of variation and heredity in our courses at Washington University Medical School.

There are several reasons for regarding these subjects as important for the student. One is the significance that may be attached to them in later clinical work, and we quite agree with Professor Huntington that the proper time for the student to acquire some insight into the fundamental principles of heredity and variation—and mutation—is just when he is familiarizing himself with the anatomy and development of the body in which these principles find expression.

Another reason why some time is given to these studies is that they throw a great deal of light on processes that take place in the normal course of development, and the hope is perhaps justifiable that they could be made to throw more light than they now do upon development in general.

Finally, since the human species is more thoroughly known than most other forms and its individuals are subject to frequent

examinations and tests, of which records are generally preserved, it follows that some of the very best material for the study of general questions of variation and heredity is afforded by man himself. This fact not only justifies, it in a sense demands, the attention of the anatomist.

These matters are presented to the student chiefly through the medium of the dissecting laboratory and the course in embryology. Dr. Terry has for a number of years used a printed form in which an endeavor is made to get a record of all the principal variations in each cadaver dissected. This appeals strongly to the student and incidentally furnishes a stimulus to the study of normal relations. The data thus accumulated ought ultimately to be valuable for their bearing on questions as to the limits of fluctuating variations and as to the correlation between the two sides of the body, and between variations at different levels and in different organs. In some cases the family histories of the cadavers have been obtained.

In the course in embryology some laboratory work and several lectures are given on *phylogeny*, variation, and heredity. An outline of the current views of heredity is presented and an attempt is made to drive home the idea that the adult form of parts as well as of the whole is, in the final analysis, the result of interactions between sets of intrinsic and extrinsic factors.

PROFESSOR E. R. CLARK:

There is, I believe, a tendency on the part of some of the teachers of anatomy in this country to look upon the course in gross anatomy as an unnecessary evil, with very little more at stake than the problem of driving into the heads of unwilling students a host of facts—to view it as a mere course in the geography of the human body. It is to help create or recreate faith in its possibilities that I desire to join this discussion.

Gross anatomy occupies a strategic position in the medical curriculum in several ways. The most obvious is that the course is one of the first in the medical curriculum. The student is taken in hand at a time when he feels that he is really starting, at last,

on his life work. He is therefore peculiarly open and ready to accept new points of view and new methods of work. For this reason we have it in our power to shape his future to an extent not possible in later courses.

Again, a strategic position is furnished by the nature of the material. Everyone is keenly interested in the make-up of the human body, so that we have the student's interest from the beginning. It is not necessary to 'shock' this interest into him by setting before him a living model. The material is gross, definite, easy to see and understand, not beyond the capacity of the average student, difficult only because of the excessive amount and the shortness of time allotted. It is of such a character that it is very simple to make of it an exciting, continuous, unified piece of investigation, and this to an extent not possible in any other course in the present-day medical curriculum.

A strategic position is also afforded by the fact that, owing chiefly, perhaps, to the definiteness of the material, it is possible to dispense with lectures, minute daily instructions, and set quizzes, thereby allowing the student the maximum opportunity to develop initiative, independence of thought and work and self-reliance. To a considerable extent he may each day plan his work, set problems, make his own discoveries and observations, and compare his findings with those of others.

There is needed on the part of the teacher imagination to see, in the course, not merely the teaching of a few dry facts, but the opportunity to play perhaps a decisive rôle in the making of future medical scientists. If we can take the attitude that our students are carrying out original investigations, rejoicing with them over their discoveries, helping them to elevate their ideals and standards of accuracy, and, above all, permitting them to develop initiative and independence, we shall pass them on with something more than merely another colorless course, and shall, according to our several abilities, have taken proper advantage of an almost unparalleled opportunity.

PROFESSOR EMMEL:

In connection with the present discussion, two aspects of the subject suggest themselves. While listening to the preceding addresses on the teaching of gross anatomy, my mind reverted to a recent conversation with one of our students. In response to my remark that he had no doubt received much inspiration from one of his former teachers in anatomy, he replied, "Oh, well, as a matter of fact, we saw very little of him. Aside from some lectures, he occasionally passed through the laboratory, but seldom stopped to talk with any of us about our work." I have been considerably impressed with the importance in the laboratory of a greater degree of contact between the student and the men of greatest anatomical and scientific proficiency rather than primarily between student and student assistant. In the laboratory, as Dr. Stockard has essentially indicated in the case of his own experience, advantage can be most adequately taken of the psychological moment arising in the course of the laboratory study both to crystallize important aspects of the subject and stimulate higher standards of scientific thought and interest.

A second phase of the subject relates to a problem which is no doubt more pronounced in some institutions than in others. When, in the case of a given anatomical structure or region, one undertakes to discuss certain related aspects of the subject, a difficulty is not infrequently encountered. If, for example, upon opening the abdominal cavity the instructor proceeds to discuss briefly with a student the embryological and functional significance of the urachus, he discovers to his discomfiture that the student knows little about the umbilical cord and has never seen the allantois. As conducive to more thorough anatomical training as well as the inculcation of a broader scientific interest, we may expand our departmental staffs and develop correlated elective courses in study and research, as elaborated by Dr. Jackson; on the other hand, it appears important to secure more definite preliminary biological training on the part of prospective medical students. In the latter case both student and instructor would be less frequently embarrassed by the discovery that a course in botany constitutes the only basis for mutual anatomical intercourse.

PROFESSOR RANSON:

As a discipline, gross anatomy is of value in developing in the student manual skill, the capacity for accurate observation, and the ability to make use of visual imagery. Others have spoken on the first two points, but the third is equally important. If the student has developed the habit of forming and carrying clear-cut visual images, he will find this faculty of the greatest use to him in his later pathological and clinical studies. The course in gross anatomy gives an excellent opportunity for cultivating this faculty. This can be done by emphasizing for the student the importance of visualizing the pictures and dissections and by the use of atlases in preference to text-books in the dissecting-room, so that the student works the information gained in the dissecting-room into these pictures and becomes thoroughly familiar with them. These pictures will then stay with him and become a part of his subconscious memory. It will then be possible for him to forget anatomy, as Dr. Jackson and others have said he must do, and yet, at any time, by turning to the atlases, it will be possible to refresh his memory on any particular point he needs to know. A few minutes spent turning over the pages of an atlas will bring back more details than would hours of reading. I think we should emphasize for our students the importance of visualizing anatomy and help them to get away from the habit of memorizing works.

DOCTOR E. R. HOSKINS:

Mr. President: Since one cannot inspire nor make a scientist out of the average medical student, the most important duty of the teaching of anatomy is to induce him to visualize and think. Our students, especially those in the East, go through most of their pre-medical courses by mere memorizing. They are lectured to and are tutored too much for their own good. It is unfortunately true that in many of the so-called best departments of anatomy in this country, students are permitted to 'pass' the course in gross anatomy from word descriptions which they can memorize

from their texts, and most students follow the line of least resistance. In these departments too little attention is given to compelling students to observe accurately and to think.

Written examinations should be given during the course. For these examinations the questions should be carefully selected by the teacher so that the students may be, if possible, forced into co-ordinate thinking. Those incapable of this should be eliminated. Questions similar to those mentioned by Dr. Jackson are of the proper sort. Drawings to be made are good examination questions also. Since student organizations keep copies of all examination questions, we should try to avoid the common error of repetition of stereotyped questions. There is too much truth in the boast of students in most schools that they can pick out before the final examination in anatomy several of the questions to be asked, simply by studying the examinations given during the previous four or five years. It is the ambition of every student to 'out-guess' the teacher on examinations, and he often succeeds.

Another matter I wish to discuss is the desirability of making a symposium on anatomical teaching a part of our annual program, for the benefit especially of the younger members who attend the meetings hoping to learn methods of pedagogy. This plan would involve a certain amount of repetition, but this would do no harm, especially since at each meeting many members are present for the first time and few attend every meeting.

PROFESSOR MURPHEY:

I have come to the conclusion that the hardest problem is teaching the student to coördinate and use his senses of sight, hearing, and touch, and I believe it has been demonstrated experimentally that facts gained through these three mechanisms will stay better than that which is learned through one only or even two.

I have found that the student could well spend some of the preliminary periods listening to a discussion of the problems that were confronting him. Students come with the idea that scientific knowledge will resolve itself into the acquisition of facts. They

should learn early that attitude and method and the cultivation of a view-point are very important in medical education.

I may say that we have used living subjects and x-ray slides as an illuminator. The best attitude to cultivate in the student is not to take anyone's statement, but to use his own powers of observation and reasoning to critically examine and decide for himself regarding any given fact. I believe that it has been proved that if the repetitions of a subject are separated by some space of time, fewer repetitions are necessary than if they are consecutive. We have satisfied ourselves by an elective course offered seniors that this is true and that such courses are very valuable.

UN CASO DE ECTOPIA CARDIACA EXTRATORAXICA

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*From Trabajo del Laboratorio de Anatomia Patologica de la Escuela
de Medicina de Caracas—Venezuela*

ONE FIGURE

1. ANTECEDENTES

En el vecindario Coco de Mono situado a dos kilómetros de la poblacion de Cúa del Estado Miranda (Venezuela), nació un niño el 30 de noviembre de 1917 a las 8.30 a.m.

Llevado de aquel vecindario a la poblacion antes citada fué llamado el doctor J. M. Quintero Arellano en union del doctor Veracoechea Briceño, médicos en ejercicio en esa localidad, a ver al niño que acababan de bautizar, diciendoles que tenia el "corazon salido."

Los referidos doctores fueron a verlo y al examinarlo encontraron un niño de término; que habia nacido hacia poco tiempo a juzgar por el cordon umbilical cuyo aspecto denunciaba que habia sido seccionado recientemente. Al descubrirle el pecho observaron que el corazon palpitaba fuera del torax; que los grandes vasos del órgano atravezaban la pared en su parte superior y media por un agujero irregular que perforaba el esternon en su totalidad.

El órgano cardiaca funcionaba visiblemente, pudiendo notarse de una manera clara las contracciones auriculo-ventriculares y percibirse un ruido suave al acercar el oido, semejante al producido por el cierre de las valvulas de aquella viscera.

A pesar de esta anomalia comprobaron que el niño tenia sus movimientos naturales, lloraba en un tono normal, y al aplicarle el dedo a los labios succionaba sin ningun inconveniente.

Segun los informes tomados por dichos doctores, el nacimiento se habia verificado el dia, hora y localidad antes mencionados;

y la familia alarmada resolvió enviarlo a Cúa para bautizarlo y hacerlo ver de los médicos.

Durante el trayecto fué descubierto repetidas veces con el objeto de enseñarlo a las personas que demostraban interes en verlo, de modo que estuvo por este motivo expuesto al frio y al sol durante mas de una hora por lo menos.

Como el órgano lo habian cubierto con un pedazo de algodón que supusieron los medicos mencionados en malas condiciones de asepsia, aconsejó el doctor Quintero Arellano cambiarlo por gaza esterilizada.

A las 6.30 p.m. del mismo día le anunciaron al doctor Quintero que el niño acababa de morir, y éste exigió de acuerdo con las autoridades locales, que se le entregara el cadáver, para el estudio de la anomalia. Consiguió su objeto al día siguiente, a las 9 a.m. y a esa misma hora lo mandó al Hospital de Ocumare, Capital del Estado Miranda, a fin de prepararlo convenientemente para su traslado a la Escuela de Medicina.

En aquel Hospital procedieron a extraerle las visceras abdominales y llenar esta cavidad con algodón formolado. Una vez preparado de este modo fué introducido el cadaver en un recipiente que contenia alcohol formolado al uno por ciento y enviado a la Escuela de Medicina de Caracas por el ferrocarril del día tres, que fué la primera ocasion de remitirlo.

Al día siguiente de su llegada, en union de uno de nosotros, se procedió a abrir el envase, encontrándose, que a pesar de la preparacion que se le habia hecho, el cadaver estaba en estado de putrefaccion, sobre todo la cabeza.

Medimos la talla que nos dió 48 centímetros de largo; la circunferencia del torax fué de 33 centímetros, el diametro biacromial de 12 centímetros y el intermamilar de 9 centímetros.

El agujero que da paso a los grandes vasos es irregular y mide dos y medio centímetros de largo por uno y medio el menor de los diámetros.

A fin de conservar la mayor parte del cadaver, procedimos a separar la cabeza, que al parecer era normal en sus diámetros y que como se ha dicho estaba muy descompuesta. El resto del cadaver, despues de hacerle algunas incisiones en la piel de los miembros fué sumergido en una solucion de formol fuerte.

Segun informa el doctor Quintero Arellano, antes de enviar el cadaver a Ocumare, hizo tomar la fotografia que acompaña a este trabajo (fig. 1).

En cuanto a los antecedentes que pudo averiguar respecto a los padres del niño, fueron los siguientes:

La madre ha gozado siempre de buena salud y tiene 20 años de edad. El padre es sifilítico y actualmente esta en tratamiento.

El embarazo pasó sin accidentes dignos de señalarse y el parto se verificó normalmente en posicion de vértice.

Todos los datos anteriormente expuestos estan tomados de la Comunicacion hecha por el Dr. Quintero Arellano a la Academia de Medicina de Caracas en las sesion de 6 de diciembre de 1917.



Fig. 1. Un Caso de Ectopia Cardiaca Extratoraxica

2. ESTUDIO ANATOMICO

En aquella misma sesion, la Academia de Medicina resolvió encomendarnos el estudio de la anomalia encontrada en la pieza depositada en el Museo de Anatomia Patológica de la Escuela de Medicina, a cuyo personal pertenecemos.

Para dar cumplimiento al encargo de la Academia, procedimos inmediatamente al estudio en cuestion, el cual fué muy dificultoso debido a la solucion de formol tan fuerte en donde se habia conservado el cadaver descompuesto, de tal manera que la investigacion sólo pudo ser practicada por nosotros valiéndonos de máscaras y anteojos protectores.

El resultado de nuestro estudio fué comunicado en una Nota a la Academia de Medicina en su sesion del 3 de enero de este año.

Inspeccion del cadáver

El cadaver esta decapitado y parecer ser un feto a termino por sus proporciones normales. Equidistante de los dos mamalones y en el centro de la pared anterior del torax, se nota el corazon procidente como una masa endurecida, en forma de cono y de color oscuro, cuyos vasos salen por un agujero irregular que existió en el punto de la pared mencionado. El eje del corazon está dirijido casi horizontalmente, un poco de arriba abajo y de dentro afuera. Se nota a los lados y en la parte mas cercana a la pared toraxica la presencia de dos pequeños abultamientos, al parecer representantes de las orejuelas: la derecha mayor que la izquierda. El color del corazon es oscuro a partir de la punta hasta el tercio superior y de alli en adelante es gris; las orejuelas son de un gris mas oscuro. En la superficie del miocardio se dibujan algunos vasos sinuosos y ramificados. La circunferencia mayor mide once centimetros y el eje es de cuatro y medio centimetros.

En la pared anterior del abdomen, a uno y otro lado, se dibujan ramificaciones venosas.

Los miembros se encuentran en estado de putrefaccion; la epidermis levantada en muchas partes y el color violaceo. Las uñas de los dedos de las manos presentan un color morado oscuro y las de los pies tienen un color amarillento.

Como era imposible hacer una investigacion necrópsica siguiendo el método acostumbrado en la Escuela de Medicina, puesto que la evisceracion del cadaver habia sido ya efectuado, y vista la necesidad de darnos cuenta de la anomalia, sin alterar en lo posible la disposicion de la ectopia cardiaca, resolvimos, despues de la inspeccion hecha, adoptar un plan de investigacion conforme con las circunstancias, para el análisis de las cavidades toraxica y abdominal y de sus relaciones con la viscera y vasos anormales.

Inspeccion de la cavidad abdominal

Siguiendo la incision hecha por los médicos que evisceraron el cadaver, empezamos por quitar mas de nueve puntos de sutura que cerraban la cavidad, encontrándola rellena de algodón. Sacado éste, no vimos en el interior ninguna viscera ni ningun gran vaso.

Inspeccion de la cavidad torácica

La ausencia del diafragma nos permitió inspeccionar el interior del torax por la misma via.

El lugar ocupado por el pulmón izquierdo estaba vacío; pero del lado derecho encontramos una masa que no pudimos distinguir claramente con la luz que nos daba la incision hecha. Tanto para averiguar este punto como para ver la disposicion de los organos del mediastino, teniendo en cuenta la mejor conservacion de la anomalia, resolvimos hacer luz por la parte posterior del cadaver.

Practicamos para esto una incision a lo largo de la columna vertebral siguiendo las apófisis espinosas; de esta manera seccionamos la piel; separamos los músculos superficiales y profundos de la region; cortamos con una cizalla las costillas izquierdas y derechas; con la sonda acanalada disecamos las adherencias de los órganos del mediastino con la columna vertebral y logramos quitar el raquis.

Desde el primer momento nos damos cuenta de que la masa que percibiamos del lado derecho del torax era el pulmon de ese lado. Advertimos igualmente que habia quedado adherido por sus inserciones anteriores una porcion del diafragma y rechazado hacia arriba probablemente, por el algodón que rellenaba la cavidad abdominal.

Vamos a indicar ahora los detalles referentes al diafragma, pulmon, y vasos cuya diseccion hemos ido haciendo metódicamente.

Diafragma. Este músculo, como se dijo, aparece muy rechazado hacia arriba y su insercion a la pared anterior del torax parece estar un poco más alta que el nivel normal.

Pulmón derecho. Disecamos la pleura que lo envuelve y observamos que tiene tres lóbulos. Guiados por la entrada del bronquio derecho en el hilo pulmonar, disecamos aquel bronquio, como también el izquierdo, que aparece cortado, y separamos un pedazo de traquea seccionada al nivel del cuello. Disecamos y seccionamos los vasos pulmonares sin poder darnos cuenta de su distincion en arteriales y venosos, debido a la fragilidad de sus tónicas y de esta manera sacamos el pulmón.

Hecha la docimasia pulmonar, comprobamos que el niño habia respirado.

Durante la disseccion anteriormente hecha, separamos un pedazo de tubo correspondiente al esófago y otro representante de la aorta descendente.

Nos dirigimos entónces al mediastino anterior y encontramos, disecando metodicamente de adelante atras, una glandula al parecer el timo, colocada en una celda situada en la linea media, y limitada, por delante por el esternón, por detras por los grandes vasos y a los lados por la reflexion de la pleura respectiva. Disecados los vasos encontramos que la pared posterior de la celda antes descrita pertenece al pericardio reflejado en ellos, de manera que el agujero que comunica con el exterior queda perfectamente oculido por dicha reflexion pericárdica.

Separamos el pericardio reflejado en los vasos y de esa manera los sacamos al exterior a travez del agujero que presenta el torax. Sólo quedó el corazón adherido al torax por un pedazo de pericardio pegado a la cara posterior, el cual lo mantiene colocado en la posicion respecto al agujero torácico, que primitivamente tenia.

Disecado el pedículo vascular, comprobamos la existencia de tres grandes vasos. En un punto equidistante de las dos orejuelas se nota la salida de dos de ellos que forman uno sólo a dos centímetros de su salida. En todo su trayecto emiten varias ramas gruesas. El tercero se desprende de un ensanchamiento que comunica con la base del corazón al lado izquierdo de los primeros nombrados, bifurcándose a cuatro centímetros de su salida. En su trayecto también emite colaterales.

Tanto al evisceracion a que fue sometido el cadaver, como la mala conservacion de los tejidos, nos impidieron darnos cuenta

exacta de la disposicion y significacion de los troncos y de sus colaterales.

Inspeccion interior del corazon

Como el corazón aparece en forma de una masa endurecida, no pudimos seguir los cortes acostumbrados para la autopsia del órgano. Resolvimos para esto hacerle un corte frontal pasando por la punta, por las orejuelas y por el lugar de donde se desprenden los grandes vasos. Hecho esto, encontramos el corazón dividido, como en el estado normal, por el tabique inter ventricular; pero en la parte inferior de este tabique existe una comunicacion anfractuosa que va del ventrículo derecho al izquierdo.

Del ventrículo izquierdo se desprenden casi en un mismo punto, separados apenas por un pequeño tabique, los dos grandes vasos primeramente mencionados.

El espesor de la pared ventricular es de tres a cinco milímetros. En su cara interna aparecen sus pilares cuyas cuerdas tendinosas se dirijen de abajo arriba, como en el estado normal; pero no pudimos determinar de una manera precisa la existencia de la valvula mitral característica, debido al estado del endurecimiento de la pieza, Ademas de aquellas columnas carnosas, se ven claramente las de segundo y tercer orden.

Con el objeto de estudiar la disposicion de la válvula mitral, hicimos en este ventrículo un corte que va de la punta a la base y que es el que hacemos normalmente para el estudio de esa válvula. Encontramos entónces que el orificio aurículo-ventricular comunica con una cavidad virtual, quizas por aplanamiento de sus paredes, de forma redondeada, de dos centímetros de diámetro y al parecer representante de la aurícula correspondiente a dicho ventriculo. Al despegar sus paredes se nota que su cavidad comunica con el tercer gran vaso de un lado, y por abajo con el ventrículo del lado opuesto.

La orejuela izquierda está subdividida en cavidades y no le encontramos comunicacion con la aurícula izquierda.

En el otro ventrículo no encontramos pilares. Los mínimos repliegues observados hacia la parte en donde debia existir el

orificio aurículo-ventricular no recuerdan por su aspecto la válvula tricúspide.

En su parte más superior se encuentra la comunicacion mencionada antes con la cavidad auricular descrita.

La orejuela del mismo lado comunica con la parte superior de ese ventrículo. Tanto este hecho como la comunicacion encontrada antes con la aurícula del lado opuesto y asi como por no haber encontrado ningun otra cavidad representante de la aurícula respectiva, nos hace suponer que la aurícula que corresponderia al ventrículo de que nos ocupamos esta sumamente atrofiada o falta por completo.

Inspeccion del esternón

Procedimos despues al estudio del esternón yendo de atras hacia adelante. Separamos una membrana, al parecer la pleura costal; desnudamos el esternón, encontrando que mide tres centímetros de largo por dos de ancho al nivel del manubrio y uno en casi toda la extension del cuerpo. Contamos las insercion de cuatro costillas de uno y otro lado. Por su parte inferior la pieza esternal termina en la linea media, al nivel de la cuarta insercion costal y se continua de alli en adelante en forma de dos ramas que se dirijen primero hacia abajo y hacia afuera para luego tomar la direccion hacia abajo y hacia adentro limitando en su conjunto un agujero de dos centímetros y medio de diámetro, al traves del cual pasan los grandes vasos del corazón. Las ramas del esternón no llegan a formar circunferencia completa, quedando entre sus dos extremidades un espacio de un centímetro de largo. La dispocision del esternón y de las ramas que lo continuan recuerda por su forma un forceps de Pajot con las ramas más cóncavas y separadas.

En síntesis, las anomalias que hemos encontrado en este caso de ectopia cardiaca extratorácica podemos resumirlas asi:

1°. El corazon se hallaba completamente fuera del torax y en la linea media.

2°. Sus vasos atraviezan un agujero formado en el esternón y limitado en su parte superior por el borde del esternón al nivel de la cuarta insercion costal y por abajo circunscrito por dos

ramas de concavidad interna, cuyas extremidades no llegan a tocarse.

3°. No encontramos sino una sola aurícula en comunicacion con los dos ventrículos.

4°. Los ventrículos se comunican por un agujero situado en la parte inferior del tabique interventricular; por tanto, no creemos que sea este agujero el representante del foramen de Panizza que existe, como se sabe, a menudo en los reptiles y algunas veces por anomalia en la especie humana, ya que la abertura encontrada por nosotros se halla en la porcion musciosa del tabique, en tanto que aquella se ha descrito por los autores en la porcion membranosa de dicho tabique, en le punto en que el septum aortico se une al septum ventricular.

5°. Dos grandes vasos salen al parecer del ventrículo izquierdo y a pocos centímetros de su salida forman uno sólo.

6°. Un gran vaso parece desembocar en la única aurícula.

7°. El orificio esternal queda ocluido perfectamente con la reflexion del pericardio en los grandes vasos.

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THE BEHAVIOR OF THE PHAGOCYtic CELLS OF THE PERITONEAL FLUID TOWARD PARTICULATE MATTER

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The local reaction in the peritoneal cavity following the intra-peritoneal injection of microscopic particulate matter such as carmine and carbon, has been studied by many investigators, and the phagocytic activities of the several types of cells involved have been closely observed. In recent years the colloidal azo dyes, such as pyrrhol blue and trypan blue, have also been utilized to demonstrate the phagocytic capacity of cells, and it is interesting to compare the behavior of the cells of the peritoneal fluid towards these much finer molecular aggregates with the results previously obtained, with the coarser particles of carmine and carbon. By such comparison, something is learned of the differences in range of activity of several phagocytic cell types, and some of the factors are suggested which must be considered in the analysis of phagocytosis of finely-divided particulate matter.

The entrance of substances into living cells is a phenomenon common to all cells. That it is conditioned by the selective action of the cells themselves is evidenced by many observations. The phenomenon of phagocytosis may be looked upon as a special case of entrance of substances, exhibited by certain more or less well defined groups of cells, in which usually the substances which are taken up by the cells are of microscopic size, and there is a microscopically visible reaction on the part of the cells. However, there is no definite lower limit to the size of the particles, and the term phagocytosis has been extended to cover the entrance of colored colloidal aggregates of various dyes, of which the size of the individual aggregates is ultramicroscopic, but

which, by reason of a change in the state of their dispersion, become visible under the microscope.

Our special interest in the experiments to be described has been in the differences of reaction shown by phagocytic cells, especially of the peritoneal fluid, towards different sizes of particles, and it may be permitted to recall briefly some of the current views in regard to the differential behavior of leucocytes and other phagocytic cells.

In explanation of the phenomenon of phagocytosis of cellular organisms, in which a phagocytic cell ingests one organism and not another, both in the same medium, the theory of positive and negative chemotaxis has been advanced (for full discussion, Metchnikoff '07). According to this theory, stated in a simple form, the ingestion of the substance depends mostly on the sensitiveness of the phagocyte to outside chemical influences. The action of the phagocytes depends upon their perception of the chemical composition of the medium surrounding the substances to be ingested. This medium may contain chemical compounds which are repellent,—the condition of negative chemotaxis, or it may contain substances which are attractive,—the condition of positive chemotaxis. Evidently the beginning of the reaction can take place at a distance from the object through the diffusion of the exciting substance.

In the case of inert non-toxic particles (e.g. carbon, carmine) the chemical stimulus operative in the case of cellular matter is much reduced, or may be wholly lacking. Here the stimulus arising from the presence of the foreign substance depends mostly on the physical properties of the particles, and is evidently operative principally when the particles come into contact with the cell membranes of the phagocytes. In such a case the action of the phagocytic cells, whether positive or negative, may be regarded as mostly dependent upon the state of irritability of their plasma membranes—the capacity of the plasma membranes for appreciating the presence of the foreign particles. That the cell membrane, by reason of its physico-chemical properties, is the essentially sensitive portion of the cell, the portion which controls the response of the cell as a whole to stimuli of various

kinds is a view that has much evidence to support it (R. S. Lillie, '14). Thus from a more general standpoint, inert particles represent but one of several forms of stimuli which cause measurable reactions in living irritable cells, and the phenomenon of phagocytosis is but one mode of reaction to external stimuli. This sensitivity of the cell membranes towards inert particles has been studied experimentally, and is found to vary under different conditions. Thus the phagocytic capacity of leucocytes in vitro towards carbon particles has been found to be greatly modifiable by physical and chemical changes in the surrounding medium (e.g. Hamburger '12). In his experiments he found that, by the addition of very minute quantities of calcium chloride, the number of leucocytes taking up the carbon particles in a certain time period was much increased, while anisotonic solutions of various substances decreased the phagocytic capacity of the cells. Urea was found to produce no constant result, while many lipid soluble substances in weak solution increased the degree of phagocytosis, and stronger solutions of the same substances decreased this activity. In such experiments the variation in the reaction towards a constant stimulus must be regarded as depending upon variations in irritability of the cell-membranes.

Other examples of the variability of reaction of phagocytic cells have been given recently by Downey ('17) in a paper in which he presents an interesting case of the experimental conditions modifying the behavior of the polymorphonuclear leucocytes and lymphocytes towards pyrrhol blue.

Mention may be made also of the several factors which play a part in the entrance into cells of dissolved and colloidal substances in general. These factors have been the subject of numerous researches from the physico-chemical standpoint (for full discussion see Höber '14), and many factors have been adduced, e.g., physico-chemical state of structural colloids of the plasma-membrane, and its state of permeability at the time of entrance of the substances, and (1) state of dispersion, (2) lipid solubility, (3) basicity (operative probably in basic vital dyes) and (4) surface activity of the substances entering. In any

particular example, any one or a combination of these factors may be operative to determine the resultant action. Likewise in the case of phagocytosis of inert particles and colloidal aggregates some of these factors must also play a part in the phagocytic response, although the exact mechanism is but little understood.

From a consideration of the foregoing, it is seen that the selective action of cells is subject to many modifying influences, and that phagocytic cells are no exception to the general rule. While it is agreed that each class of phagocytes has a normal limited range of activity, there may be many alterations and extensions to this range due to variable intracellular factors, changes in the surrounding medium and to the nature of the stimulus. All this is well recognized in the case of phagocytosis of microorganisms but much less realized in the phagocytosis of particulate matter.

EXPERIMENTS

In our experiments we have observed the phagocytic response of the cells of the normal peritoneal fluid, especially to the azo dye trypan blue, carbon particles in suspension, filtered lithium carmine and colloidal iron. In making the examination of the cells, the peritoneal fluid was withdrawn with a fine pipette and examined under the microscope immediately, in order to forestall the action of the staining factor in the dyes.

In the normal peritoneal fluid of the albino rat, the most prominent cell-types are,—1) coarsely granular basophiles, 2) coarsely granular eosinophiles, and 3) non-granular mononuclear cells. The basophiles are the largest, measuring often 15–20 μ in diameter in smear preparations, with round nucleus 5–7 μ in diameter, and according to Kanthack and Hardy ('94), they form 5–10 per cent of all nucleated cells. The other two types are present in approximately equal numbers, but considerable variation in relative proportion may occur. The eosinophiles are characterized, in addition to their specifically staining granules, by the nucleus being frequently ring shaped. The nucleus is really linear in form, and it is bent into a circular form with ends sometimes approximating, sometimes overlapping,

thus forming an open circle. The granules are seen filling the cytoplasm both inside and outside the nucleus. The non-granular cells are of varying sizes. The smallest have a rounded nucleus with a very narrow film of cytoplasm around it, and are often referred to as lymphocytes. The largest also have a rounded nucleus, which is frequently flattened or slightly concave on one side, and these are the typical phagocytic macrophages of the peritoneal fluid. But there are many of intermediate size, and it appears that all are growth stages of one type of cell, probably originating in the *tâches laiteuses* of the omentum. Detached mesothelial cells are sometimes seen in smear preparations, but these are rare. Ordinary polymorphonuclears are generally absent in the normal peritoneal fluid, but quickly appear as the result of injection of various substances. Erythrocytes are lacking or present in very small numbers.

In the course of our experiments with carmine and carbon we have found in certain instances that the function of phagocytosis was evidenced by all sizes of non-granular cells, but always in such cases relatively more by the largest ones. In many examples phagocytosis was shown only by the largest non-granular cells. Minute particles have sometimes been seen in the mesothelial cells, but it is probable that their presence is only transient. There is no doubt that the particles can readily be passed through these cells, and we have regarded the particles that we have seen in them, as not segregated there in the manner of true phagocytosis. The basophiles and eosinophiles are apparently not phagocytic for the substances we have used. The amount of peritoneal fluid in the albino rat is normally very small, and one obtains but a few drops when a fine cannula or capillary tube is introduced.

1. If 5 cc. of 1 per cent fresh colloidal trypan blue, made up in physiological salt solution, be injected into the peritoneal cavity of a 150 gm. albino rat, smears of the peritoneal fluid, made at the end of 24 hours show slight or no phagocytosis. In some experiments not a single cellular element was seen containing the dye, while in other experiments only the faintest blue granules could be seen in the largest mononuclears. On the other hand,

certain cells of the body such as the clasmatocytes of the testis show a very evident amount of the dye.

If we inject 5 cc. of a suspension of filtered lithium carmine (Kiyono, '14) into the peritoneal cavity of a second rat, smears of the peritoneal fluid taken in 24 hours show phagocytosis in numerous cells, both macrophages and polymorphonuclears, many of them loaded with masses of carmine. The clasmatocytes, the phagocytes within the connective tissues of the body, show the dye in a much slighter degree than after trypan blue injection.

Our interpretation of these results is that we are dealing with two relatively non-toxic particulate systems, each inducing phagocytosis according to the degree of irritation which it produces. The colloidal particles of trypan blue are of such small size that they are able, within the time period, to induce but slight visible phagocytosis within the cells of the peritoneal cavity, though it is undeniable that numerous ultramicroscopical particles may be present which are not revealed by the microscope. The rapid diffusion of the colloid through the body, however, brings the dye particles in contact with a number of cell-types which are able to take up the minute particles—a phenomenon explainable by presupposing a lower threshold of irritability in these cells.

On the other hand, the carmine particles in suspension present a wide range in particulate size, the largest of which are certainly able to cause considerable irritation, as evidenced by the magnitude of the phagocytic response within the peritoneal cavity. The smaller carmine particles are in part diffused throughout the animal body in a manner similar to the colloidal dye particles, thus explaining the presence of the carmine within the connective tissue phagocytes. At the end of 24 hours, the trypan blue animals are colored a distinct blue and the carmine animals are colored pink, but it would seem that less of the carmine than of the trypan blue finds its way to the superficial tissues. In each case, while much of the dye is thus rapidly segregated in various cells of the body, part of the free circulating dye soon begins to be excreted through the kidneys, and the dye particles are seen in the cells of the cortical portion of the kidney tubules.

2. Another and more striking way of showing the difference in reaction is by injecting simultaneously large and small-sized particles. We have used for this purpose filtered India ink and fresh trypan blue, 2.5 cc. of each, mixed and injected together. When the peritoneal fluid is examined at the end of 24 hours, the carbon particles are present in great numbers of cells, but no blue is visible in any of the cells. When smear preparations are stained and examined, numerous polymorphonuclears and macrophages are found, containing an abundance of the black particles but no blue.

3. For comparison, we may briefly detail the reaction to carbon particles. Carbon has been extensively used for this form of experiment, and the reaction has been frequently studied, e.g. Buxton and Torrey ('06). We have used finely powdered lamp black, rubbed up in normal salt solution, three grams of the former to 100 cc. of the latter. The suspension was filtered before being injected. The usual volume injected for 150 gram animal was 3 cc. For one to two hours after the injection of the carbon suspension there are but few cells to be found on account of the dilution of the peritoneal fluid, and very little phagocytosis has taken place. At two hours after injection, however, macrophages may be found which already show inclusions. At this time polymorphonuclears begin to appear and become increasingly numerous. The macrophages also increase in number. During 4-6 hours after injection both polymorphonuclears and macrophages take up the particles more and more. The macrophages continue to increase in number and ingest not only free particles but also some of the polymorphonuclears which already contain carbon. At the end of 24 hours the macrophages are numerous and all contain masses of carbon particles, while a few contain in addition the remains of one or even two polymorphonuclears with the particles still within them.

Surveying the result of injection of these three substances, trypan blue, filtered lithium carmine and carbon suspension, we find that we obtain three grades of reaction. The carbon particles produce the most rapid and marked effect. Macrophages already show inclusions at the end of two hours, and numerous

polymorphonuclears appear at this time and assist in the phagocytic reaction. At four and six hours, both macrophages and polymorphonuclears show increasing amount of phagocytosis and continue their activity thereafter. At 24 hours after injection there is an abundance of fluid, containing great numbers of cells, in the peritoneal cavity. The trypan blue produces very little effect. Relatively few polymorphonuclears appear and these do not take up the dye, while phagocytosis by macrophages proceeds very slowly. The amount of free fluid in the peritoneal cavity at the end of 24 hours is little more than normal. Filtered lithium carmine holds an intermediate position. Its presence calls forth the polymorphonuclears but these do not appear in such large numbers as after the injection of carbon particles, and phagocytosis is slower in beginning. At eight to twelve hours particles are seen in both macrophages and polymorphonuclears, while at 16 hours the reaction is still more evident. At the end of 24 hours, however, though many polymorphonuclears are to be seen, only a small percentage show inclusions of carmine. The macrophages are practically all laden with carmine, and some contain, in addition, a polymorphonuclear with carmine particles in it. The amount of fluid in the peritoneal cavity at this time is greater than normal or after trypan blue injection.

Judging from these comparisons it would seem that the size of the particles was an important factor in determining the character and rate of the phagocytic reaction in the peritoneal cavity.

4) Experiments were then tried in the attempt, through alterations in the physical state of the colloidal trypan blue, to induce more rapid phagocytosis. Alteration in the direction of enlargement of the molecular aggregates may be effected in several ways, such as by allowing a colloidal suspension of trypan blue made up in salt solution, to stand in the sunlight for a number of weeks, or by boiling a fresh colloidal suspension for several minutes. In these ways the colloidal properties are in part destroyed, and a true suspension is obtained. We now find that the injection of such a suspension of trypan blue into the peritoneal cavity produces results differing greatly from those obtained

when the fresh trypan blue is injected. Thus in the animal receiving injections of the boiled trypan blue, we find that a greater part of the material remains within the peritoneal cavity and internal organs, and only slight diffusion takes place through the superficial parts of the body. The animal does not become a deep blue, but takes on only a pale bluish or purplish coloration. This difference in diffusibility is looked upon as due to the increased size of the molecular aggregates (Evans and Schulemenn '14). Examination of the peritoneal fluid of such an animal, 24 hours after injection, shows that a more extensive phagocytosis has taken place, and that there is a greater amount of free fluid within the peritoneal cavity than after the injection of the fresh colloid. In addition to the macrophages, there are also many polymorphonuclears present. The phagocytosis is confined practically to the macrophages, although we have occasionally seen a little of the blue in the polymorphonuclears. This experiment is of interest in demonstrating that, while in one case the small molecular aggregates of the fresh colloid are nearly incapable of inducing phagocytosis, the larger particles of the true suspension are able to bring about a more rapid reaction. The reaction in this latter case may be looked upon as a response to the irritation produced by the larger molecular aggregates of the suspension.

5) Similar results were obtained by making use of colloidal iron, instead of trypan blue. When a rat is injected intraperitoneally with 2 cc. of colloidal iron, the peritoneal fluid cells, after 24 hours, showed no phagocytosis. When a rat is similarly treated with 2 cc. of iron suspension obtained by precipitating the suspensoid by a small amount of sodium chloride, the peritoneal fluid cells showed much phagocytosis. The visible reaction evidently depends greatly on the size of the particles in the injected substance.

Although little or no phagocytosis of the fresh trypan blue is visible in 24 hours after injection, if a longer time period be allowed, the reaction becomes quite evident. Thus, it is found, that although there may be little visible phagocytosis even in 48 hours, if one waits for 72-144 hours, the macrophages show

a considerable amount of the dye. From this it would seem, at first sight, that the minute particles of the fresh suspensoid are themselves able to cause a visible phagocytic reaction, provided the time period be sufficient. Other complicating factors enter into the reaction, however, for it is quite probable that there is a gradual agglutination of the colloidal aggregates due to the various electrolytes present in the peritoneal fluid, acting at body temperature. These larger particles could then be more readily taken up by the cells.

SUMMARY

Viewing these various observations on the intraperitoneal injection of several forms of finely divided matter, we find a graded series of reactions which depend chiefly on the size of the particles introduced. We may arrange these substances in order of particulate size: 1, Carbon particles in suspension; 2, Filtered lithium carmine; 3, Boiled trypan blue; 4, Fresh trypan blue and other colloids.

In the case of the first two substances, both macrophages and polymorphonuclears take an active part in the phagocytosis. This reaction is more prompt in the first than in the second case. The visible phagocytic reaction to injections of carbon suspension is well advanced in from four to six hours and to carmine in from eight to twelve hours. In the reaction to the third substance, the same types of cells are present. Not until the end of 24 hours, however, do the macrophages begin to show a definite amount of the dye while the polymorphonuclears at no time take part in the phagocytosis.

After the injection of colloids, there is practically no visible reaction before 24-36 hours. In the transudate there are again both macrophages and polymorphonuclears, but the total fluid volume is less than in the preceding instances and the total number of polymorphonuclears is small. Thus it is seen that the visible phagocytic reaction takes place most rapidly in the case of the largest particles and that the rate decreases as we go down the series, until in the case of colloids the size of the molecular aggregates is at the lower limit of size necessary to stimulate the macrophages of the peritoneal fluid to phagocytosis.

Analyzing these reactions from the standpoint of the cells, we find that the behavior of the polymorphonuclears varies with the size of the particles. The larger the particles, the more rapid the appearance of the polymorphonuclears, and the sooner they begin phagocytosis. In the case of finer particles, as in boiled trypan blue, they appear but apparently take little or no part. In the reaction to fresh trypan blue, they are present in still smaller numbers.

The behavior of the macrophages is similarly graded. In 24 hours after the injection of the coarser substances, they are loaded with the particles. In the same time-period after the injection of trypan blue, they show little or nothing of the dye.

Comparing the range of activity of the polymorphonuclears and the macrophages, we find that the former take up sizes only within certain limits, while the macrophages ingest particles both larger and smaller than those taken up by the polymorphonuclears, occasionally even devouring the polymorphonuclears themselves. The coelomic macrophages are probably to be regarded as a more primitive cell type than the polymorphonuclears of the blood and have retained a wider range of phagocytic activity. F. A. Evans ('16) comes to similar conclusions when he asks "Does this mean that the histogenous macrophage will take any material mass, regardless of size, while the polymorphonuclear cell is selective for particles not too large or too small?"

In experimental work dealing with the reactions of polymorphonuclears in the blood stream, it has been emphasized that mechanical churning may be a factor in preventing the phagocytosis of particulate matter. (Downey '17 p. 446.) While this factor is no doubt operative in the case of large particles such as carbon and carmine, it cannot be held entirely accountable for the behavior of the polymorphonuclears toward the small molecular aggregates of trypan blue. For within the peritoneal cavity where the factor of mechanical agitation is largely negligible, we find that although the polymorphonuclears take up particles of carbon and carmine, they do not take up the trypan blue any more than they do in the blood stream.

We would, therefore, emphasize that the size of the molecular aggregate is an important additional factor in determining not only the rapidity and degree of phagocytic response to inert particulate matter within the peritoneal cavity, but also determines in large part the type of phagocyte predominating in the reaction.

We wish to thank Dr. Paul A. Lewis, of the Henry Phipps Institute, University of Pennsylvania, for kindly supplying us with the trypan blue used in these experiments.

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A STUDY OF A 7 MM. HUMAN EMBRYO; WITH SPECIAL REFERENCE TO ITS PECULIAR SPIRALLY TWISTED FORM, AND ITS LARGE AORTIC CELL-CLUSTERS

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This embryo, obtained after hysterectomy, was very kindly sent to me, with the chorionic vesicle intact, by one of my former students, Dr. Joseph S. Hume of Norfolk, Virginia. It had been placed in a 10 per cent formalin solution about an hour after the operation. The embryo would seem to merit a brief separate description by reason of its extreme spiral form (fig. 1), and its unusually numerous and large aortic cell-clusters (fig. 7). The study of this embryo supplies important data for the interpretation of these two characteristics, here greatly accentuated, present in small and variable degree in practically all young human embryos of a certain stage of development. The fact that we possess the requisite data also for a fairly close computation of its age, adds to the importance of this specimen.

Chorionic vesicle. The complete ovum had an oval shape measuring approximately 20 mm. by 12 mm. With the exception of a small, approximately circular, equatorial area, it was thickly covered with villi. There was no macroscopic evidence of any pathologic or abnormal conditions. Under microscopic examination the chorionic villi, the amnion, the mucous tissue of the umbilical cord, and the trophoblast islands appear perfectly normal. There is no round cell infiltration in the membranes, nor are any leukocytes present among the trophoblast cells.

Yolk-sac. Due to my special interest in the histology of the human yolk-sac, I was very anxious to obtain and study the sac of this specimen. On opening the chorionic vesicle the embryo was immediately noted, but the umbilical vesicle could not be

discerned. This was the more surprising since this vesicle, attached to its stalk, is generally quite conspicuous in its usual position just forward of the head. On exploring the exocoelom a considerable, though judging from Mall's description,¹² not abnormally excessive, reticular magma ('magma réticulé') composed of delicate fibers was encountered; but the yolk-sac could not be disclosed. I noticed, furthermore, that the embryo had suffered a complete spiral twist (figs. 2 and 3) in its post-cardiac portion, that the umbilical cord was exceptionally short, and that the amnion was closely adherent to the chorion in a narrow annular zone about the point of attachment of the body-stalk to the chorion. Since the complete series of sections of the embryo, including the placental pole of the cord, the adjacent portion of the fetal placenta, and the umbilical celom, reveal no trace of the yolk-sac or stalk, I conclude that the sac had become caught between the amnion and the chorion and had suffered dissolution. If this conclusion is correct, we are led to the further conclusion that, since the sections show no clear indication of abnormality (figs. 4 to 6), the yolk-sac represents no essential factor in determining normal ontogeny at least after the third week of development. This calculation assumes that the consummation of the disintegration of the sac, under the conditions obtaining for this embryo, required about ten days.

Age of the embryo. The embryo lay on its right side (fig. 2) with the umbilical cord passing over the left side. The longest measurement was along the nape-breech line, 7 mm. After transferring the specimen to alcohol during the paraffin embedding-process it shrunk to about 5 mm. Using the greatest length, 7 mm., for determining the age by length by comparison with standard series of embryos (His,³ Keibel und Elze,⁹ Mall,¹⁰ Triepel¹⁷) it falls somewhere between 26 and 34 days. Mall¹¹ computed the age of a 7 mm. embryo (No. 208) at 26 days. Triepel¹⁷ ascribes an age of 34 days to the same embryo. Our embryo corresponds most closely with Embryo A (7.5 mm.) of His's collection, which he estimated to be from 27 to 30 days old. It corresponds closely in external appearance also with Embryo 112 of Keibel's collection (Normentafeln, Keibel und Elze,⁹

fig. 9, plate 6) the greatest length of which is given as only 5.3 mm., though it has thirty-six somites and four branchial arches, and is described as being slightly less developed than His's Embryo A.

The data pertaining to our embryo (Hume) are: Last menstrual period began August 15; uterus removed October 3. The greatest possible age, therefore, allowing seven days for a period probably unfavorable for fertilization, could be only 42 days. Computing the age according to the conventional formula of His, on a basis of 28 days for the menstrual cycle, we arrive at only 21 days. To this result, however, should be added at least 7 days to allow for the passage of the segmenting ovum through oviduct and the resulting inhibition of the omitted menstruation, giving 28 days. The latter result harmonizes more closely with the revised serialations of Keibel und Elze⁹ and of Triepel,¹⁷ and we may regard this embryo as entering upon its fifth week of development. It is interesting to note that the interval between the lapsed menstruation and operation is the same (21 days) as the corresponding interval in the case of the aborted embryo of 7 mm. of Mall's collection.

Gross morphology. A very striking feature about the gross form of the embryo is its extreme spiral twist, the main element of which is post-cardiac, chiefly pelvic; but the entire embryo is to some extent involved. Reckoning from the tip of forebrain to tip of tail, the embryo makes one complete spiral turn. The only other embryos described or illustrated, as far as I am aware, as spirally twisted to a similar degree, are the Fischel embryo of Hochstetter's Collection (fig. 44, Keibel and Mall's Embryology¹⁰), and the Keibel embryo No. 112 (fig. 9, plate 6, Keibel und Elze's Normentafeln⁹). However, neither of these embryos is twisted to the same extreme degree. Moreover, the Fischel embryo (4.02 mm.), which most closely resembles our embryo with respect to the spiral twist, except that it has a sharper nuchal flexure, thus bringing the forebrain over the hind limb-bud, is certainly somewhat younger. Judging from the number of branchial arches (the fourth is vaguely discernible), the condition of the maxillary process, the character of the rhomben-

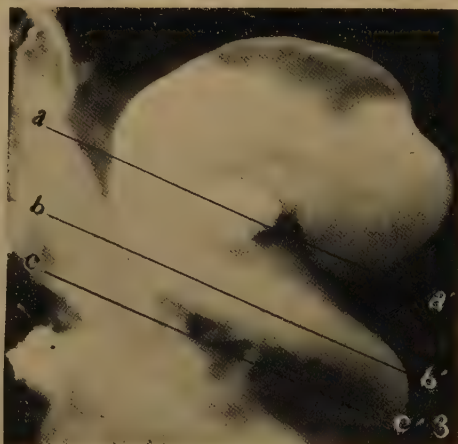
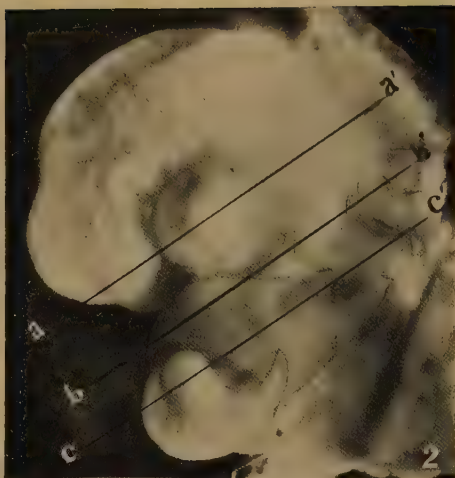
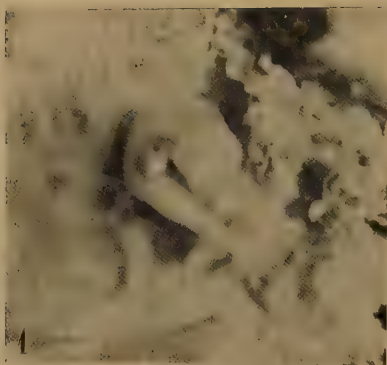


Fig. 1. View of embryo from right side, attached to chorion. It is sharply curved about the neck region, so that the tip of the forebrain touches the umbilicus. It is also twisted through a complete spiral, the mid-dorsal line coming into view caudal to the right fore limb-bud, and the left hind limb-bud showing below the pelvic flexure. The rhombencephalon, the eye, and the right vena capitis lateralis are also conspicuous; and certain of the nuchal and pelvic myotomes may be seen. Approximately thirty-eight somites could be counted. The chorionic villi are seen beyond the reflected edges of the opened vesicle. This is the view obtained when the embryo was turned on the short umbilical cord so as to expose the side opposite to the one shown when the embryo was in its more natural position as in figure 2. In this position it could only be maintained by force. When detached from the chorionic vesicle, by cutting from the wall of the vesicle a square piece of tissue including the area of attachment of the umbilical cord, the embryo assumed the position shown in figure 3, when the right cephalic surface was turned uppermost. Photo. $\times 3$. All photographs were made by Mr. F. L. Foster.

Fig. 2. Left side-view of embryo. The left ventricle and the bulbus cordis are conspicuous. The anlagen of the cerebral hemispheres, the eye, the rhombencephalon, three branchial arches, the umbilical cord, the hind limb-buds and the tail are also clearly outlined. The photograph was retouched so as to bring into sharper relief also the fourth branchial arch, the left fore limb-bud and the otocyst with the short ductus endolymphaticus. Magnification $\times 8$. The lines a-a', b-b', and c-c' indicate approximately the levels of sections in figures 4 to 6.

Fig. 3. View of right cephalic surface. The mass to the left consists of amnion above, and fused amnion and chorion below. The right fore limb-bud has become pushed forward by the spiral twisting and turned so as to bring its originally ventral border on a line parallel with the ventral surface of the pharynx. Just above the branchial arches may be seen through the translucent tissue the vena capitis lateralis. Photo $\times 8$.

Fig. 4. Section at approximately level a-a' in figures 2 and 3, just below the point of bifurcation of the trachea. This is the point where the single-cell 'angioblasts' (hemoblasts) and the smaller cell-clusters ('blood-islands') begin to appear ventrally in both aortic roots. The section shows also the base of the right fore limb-bud, the right brachial plexus, the esophagus, the left ventricle, the bulbus cordis, the inferior vena cava, the left duct of Cuvier, the liver with the ductus venosus dorsally, and the telencephalon with the right olfactory placode. The celom contains considerable blood at the right. Photo $\times 15$. (In comparing the photograph of this section with fig. 2 the top should be turned to the right; with fig. 3, to the left.) (In the process of paraffin embedding the specimen changed its shape somewhat, chiefly through accentuation of the several flexures, so that it no longer corresponds exactly with the form shown in the photographs 1 to 3, in consequence of which the level of sections cannot be indicated with absolute precision in the latter, nor any longer quite accurately with straight lines. Previous to embedding the embryo had been stained in toto with Delafield's hematoxylin. It was sectioned at 10 microns.)

Fig. 5. Section approximately at level b-b', figs. 2 and 3, showing left fore limb-bud below. (To compare with fig. 2 the top of the figure should be turned to

(Continued on page 484)

(Continued from page 483)

left; with fig. 3, to right.) Five spinal ganglia are shown; also the mesonephros, with the post-cardinal vein dorsally. The section passes through the point where the yolk-stalk was attached to the primitive ileum (shown in transverse section as minute opening at extreme tip of mesentery). In the lower portion of the mesentery are shown the vitelline arteries (superior mesenteric artery). This portion of the celom contains considerable blood. The aorta is completely filled with blood. Within the umbilical cord, to left of mesentery, is shown the umbilical vein. Adjacent sections contain the largest of the aortic cell-clusters (fig. 7). Photo $\times 15$.

Fig. 6. Section approximately at level c-c', figs. 2 and 3, through the length of the umbilical cord, showing point of reflection of amnion onto cord, below at the left. (To compare with fig. 2, turn top of figure to left; with fig. 3, to the right). The celom contains much blood; the blood-cells are perfectly preserved and entirely normal. On either side of the umbilical celom are shown the large umbilical veins. The ventral ramus of the aorta is the inferior mesenteric artery. Note the compressed notochord; it is as wide as in fig 5, where the section passes very obliquely. Photo. $\times 15$.

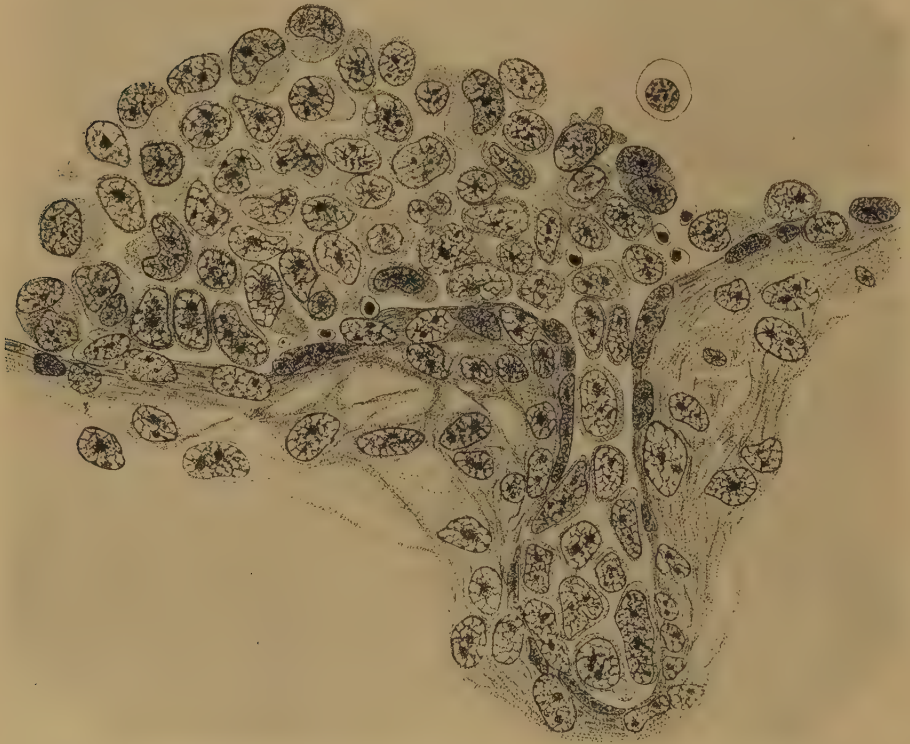


Fig. 7. Drawing of large aortic cell-cluster in relation to superior mesenteric

cephalon, the number of segments (approximately 38), and the stage of development of the limb-buds, our embryo is more nearly of the stage of development of the Keibel embryo No. 112 (5.3 mm.). However, a comparison of my sections with those published by Keibel und Elze shows a thicker and more condensed myocardium, and a more advanced stage in the development of the liver and the pancreas, which conditions bring the actual age of our embryo nearer that of the Embryo A of His's collection.

The inclusion by Keibel and Mall¹⁰ of the Fischel embryo in a series purporting to be typical warrants the conclusion that they regarded it as normal and representative for this stage of development. However, the fact that our embryo, of a clearly later stage of development, shows even a greater degree of spiral twisting, would seem to contradict the logical deduction that the peculiarity is limited to a certain restricted early stage of development. Nothing in my sections either of the embryo or the chorion, exclusive of the blood content of the celom, which may have resulted from operative trauma, suggests any pathologic condition. The red blood-cells are beautifully preserved and perfectly normal; there is much mitosis especially in the brain and spinal cord, and there is no tissue dissociation or round cell infiltration anywhere. But the body-stalk was abbreviated to such an extent that the amnion fused with the chorion at its placental terminal. Our embryo is accordingly characterized by an unusually short umbilical cord. I conclude that the spiral twist of the embryo is the necessary mechanical consequence of the shortened body-stalk (fig. 6), the result of an attempt to accommodate its lengthening form about a too restricted attachment to the chorion.

artery, 200 microns cephalad of fig. 5. Note the small erythrocytes (microcytes) at right. Above, at the right, is shown a normal-sized erythrocyte; immediately below this cell is a binucleated hemoblast; to the left of the latter appears a hemoblast in ameboid activity. The drawing only shows the cells at one level; in the section the cluster appears more compact due to the cells of adjacent levels coming into view. The preceding sections of the ventral ramus show this vessel free of cells; hence the cluster projects only along the caudal wall of the mouth of the superior mesenteric artery. $\times 1000$. Drawing by H. C. Cox.

The question then arises whether such an embryo can develop normally. If the umbilical cord should have failed subsequently to lengthen considerably, the fetus probably would have become malformed caudally, or perhaps even suffered amputation. Among the anomalies described none seem to answer exactly to the requirements of such a process, nor have any to my knowledge been thus interpreted. But the incidental interference with the placental blood-supply in such cases might result in certain of the various moles and merosomatous monsters which have been described. In the region overlying the caudal limit of the umbilicus (fig. 6), the notochord seems to be flattened, as if by undue pressure (compare fig. 6 with fig. 5), while the spinal cord and other organs in this region appear to have a normal shape; but in consequence of the slight transverse obliquity of the sections it seems unsafe to make any very definite statement in this regard. Moreover, the lumen of the central canal is unduly constricted towards its caudal extremity by a close apposition of the lateral walls, which condition may indicate a slight abnormality. The rhombencephalic brain fragmented extensively in sectioning and mounting, but this fact does not necessarily indicate abnormality of this tissue, in view of the apparent integrity of the constituent cells.

Aortic cell-clusters

Aortic cell-clusters have a special importance at this time on account of their bearing on the much mooted question of the hemogenic capacity of endothelium. The embryo under consideration contains such clusters in unusual size and abundance for an embryo of this stage of development (fig. 7). Minot¹⁴ was the first to describe aortic cell-clusters in human embryos, in stages of from 8 to 10 mm. length. But his only illustration (fig. 368, Keibel and Mall's Embryology¹⁰) shows only four cells; nor does his description of these cell aggregations allude specifically to larger clusters; we may therefore infer that the clusters seen in these stages by Minot were only of the smaller variety. In a 5 mm. human embryo (Watt's embryo) in my collection,

previously described,⁴ no aortic cell-clusters occur, though occasional endothelial cells can be seen separating from the wall of the aorta and assuming hemoblast characteristics. Also in a 13 mm. human embryo (Crenshaw embryo) of my collection no aortic clusters, other than occasional groups of two or at most four cells, occur. The available evidence from human embryos indicates that the clusters of the present embryo are of quite exceptional size and abundance.

Minot¹⁴ regarded the cells of these clusters as hemoblasts which had become aggregated along the ventral portion of the aorta near the points of origin of the larger ventral rami. The mechanical factors involved were presumably conceived to be the force of the blood stream moving towards the ventral branches of the aorta, and the adhesive properties of the cytoplasm of the involved hemoblasts.

Van der Stricht¹⁶ had previously reported comparable aortic cell-clusters in the bat, and Maximow¹³ in the rabbit; and both regarded them as endothelial differentiation products. Emmel² subsequently described similar clusters for pig embryos of from 6 to 15 mm., and interpreted them as endothelial derivatives resulting from the presence of toxic stimuli, conceived as having their source in the degenerating ventral segmental rami, and the included blood-cell content, of the abdominal aorta. Jordan likewise described these clusters for pig embryos of from 10 to 12 mm.,⁶ and in mongoose embryos of from 5 to 7 mm.,⁸ and reported them also in chick and turtle embryos.⁷ He only regards them as the expression of a normal hemogenic function of young endothelium. Danchakoff¹ also had previously reported them in chick embryos; and Sabin¹⁵ now describes comparable structures in the living chick embryo of the second day grown in Locke's solution.

Van der Stricht regards the cells of the clusters as leukocytes; Emmel² regards them as 'macrophages;' Maximow,¹³ Minot,¹⁴ Jordan^{6, 7, 8} and Sabin¹⁵ as hemoblasts (erythroblasts). Our embryo offers a very favorable material for the demonstration of the endothelial origin of these clusters, and of their erythropoietic function.

The larger clusters are found along the ventral portion of the aorta from a point just behind the level of fusion of the dorsal aortic roots to the level of the inferior mesenteric artery (fig. 6), a distance of about 1.8 mm. They are larger and more crowded about the level of the superior mesenteric artery (figs. 5 and 7). Just forward of the level of the fusion of the dorsal aortic roots for a short distance, at about the level of bifurcation of the trachea (fig. 4), occasional cells may be seen rounding up singly and separating from the endothelium as hemoblasts. The number of larger clusters in the abdominal aorta is eight. Beside these there are also five smaller clusters, and a number of groups of only several cells and occasional single cell 'clusters.' The largest groups are in close spatial relationship with the three chief ventral rami, the celiac, superior mesenteric and inferior mesenteric arteries. In each of these cases some of the cells extend for a short distance into the ramus along one side (fig. 7). In contrast with the clusters generally in the pig and the mongoose embryos, where they have a more or less spheroidal shape, in this human embryo they have a generally flattened shape with scattering cells peripherally. The group in relation to the superior mesenteric is an exception, its shape being roughly oval (fig. 7).

Just forward of the level where the aorta divides into the umbilical arteries there occur also several encapsulated cell-clusters. Similar clusters have been described by Emmel² in the aorta of the pig embryo and by myself^{7,8} in the inferior vena cava of the 12-day loggerhead turtle embryo. The larger encapsulated cluster in our human embryo consists of a group of irregular mesenchyma-like cells interspersed among which are a few spheroidal hemoblasts and a few erythroblasts, the whole group being enveloped by an endothelioid membrane except at its proximal pole where the central mass is continuous with the underlying more condensed mesenchyma. The capsule of the cluster is continuous laterally with the endothelium of the aorta. One of the smaller clusters lies directly over an atrophied ventral ramus. In my former studies^{7,8} I interpreted these clusters as differentiating invaginated areas of ventral endothelium and

periaortic mesenchyma. The two clusters here described would seem to confirm the accuracy of this interpretation. The cause of the invagination may be conceived to be the mechanical effect of tissue shrinkage following atrophy of a ventral ramus, thus pushing into the aortic lumen the endothelium and enveloping mesenchyma overlying the area of shrinkage.

Another interesting and instructive 'cluster' of this region consists of a single encapsulated cell (hemoblast) similar to those described for the mesenchyma of the mongoose⁸ (fig. 14) and the pig embryos, and there tentatively interpreted as originating from a binucleated hemoblast, one nucleus of which with its enveloping cytoplasm differentiated into a hemoblast, the other into an endothelial cell. The aortic 'cluster' here specified also adds plausibility to this interpretation; here a binucleated hemoblast differentiated from the endothelium, and then redifferentiated into an endothelial cell enclosing an erythroblast.

To return to the larger naked clusters; these shade at some point on the proximal pole into endothelium-like cells and then into the underlying more condensed mesenchyma. Since these clusters are relatively very large, flattened and more or less scattered, one can hardly apply to them exactly the same mode of origin outlined for the encapsulated clusters. These larger clusters are clearly differentiation products of the endothelium, the latter replenished from the underlying hemopoietically active mesenchyma. The cells of the clusters include hemoblasts, and more peripherally a few erythroblasts and erythrocytes (fig. 7). More centrally, and mingled with the more regular hemoblasts are also many cells, in some cases including the majority, which are of less regular shape and contain bean-shaped, bi-lobed, and irregularly lobed nuclei. Some can be seen in ameboid activity (fig. 7). A few cells also may be seen in mitosis. I incline to interpret the lobed nuclei as stages in amitotic division. Indeed a complete series of stages of amitotic division of these cells can be arranged, and it is difficult to avoid the conclusion that the prevailing mode of division here is amitotic. This conclusion is strongly supported also by the following observation: Certain of the nuclei divide very unequally, the smaller moiety being

represented by a mere spheroidal bud. Corresponding with this nuclear size-difference there occur peripherally to the cluster, scattered among normal sized erythrocytes, numerous much smaller erythrocytes with minute nuclei (microcytes) (fig. 7).

A point of prime importance in connection with this and other recent studies,^{6,7,8} is the close correspondence of my ideas regarding the hemogenic capacity of endothelium (based upon the study of sections of the yolk-sac of the pig embryo⁵ and the mongoose embryo⁸ and of certain intraembryonic blood-vessels including the aorta) and those arrived at by Sabin¹⁵ as a result of her studies of the living chick-embryo. Indeed her description of the manner in which certain of the endothelial cells lining the blood-vessels of the area vasculosa of the chick embryo of the second day project into the lumen, become filled with basophilic granules (hemoblasts) and then develop hemoglobin (erythroblasts) is substantially identical with my description for a comparable process in the yolk-sac of the pig embryo of 10 mm. and the mongoose embryo of 5 to 7 mm. The only obvious difference is that in the latter material the hemoblast generally separates from the endothelial wall; though occasionally here also it may become bi- or quadri-nucleated ('blood-island') before separating from the wall. And her further description of how such a 'unicellular blood-island' in the yolk-sac vessels (area vasculosa), vitelline veins and arteries, and the *dorsal aorta* divides 'and the mass is increased also by the addition of other cells which *differentiate from the endothelium* in the neighborhood and creep along the wall to join the first cell' (p. 202), forming 'a yellow syncytial mass projecting into the lumen of the vessel,' from the surface of which 'red cells break free from the mass and float away in the blood-plasma,' corresponds essentially to my conception of the origin and fate of the aortic cell-clusters as formulated from my studies of sections of mammalian embryos. With the admission, then, on the part of former adherents to the 'angioblast theory of His' that the blood-vessels of the embryo differentiate from the intraembryonic mesenchyma and that blood-cells may differentiate from endothelium, little of importance remains of this tenacious hypothesis.

The new work of Sabin¹⁵ supplies valuable additional data also to the advocates of the monophyletic theory of blood-cell origin. Surely her conclusion that since 'all of the blood-cells of the chick of the second day of incubation can be seen to have hemoglobin in the living chick . . . they cannot be considered as forerunners of white blood-cells' (p. 204) has no meaning as an evidently intended argument in opposition to the monophyletic theory when read in juxtaposition with her preceding statement that the endothelial cell in the process of differentiation into a unicellular blood-island 'becomes filled with basophilic granules and develops hemoglobin' (p. 202). No one to my knowledge seriously proposes that leukocytes differentiate from erythroblasts. The monophyletic theory, as I understand it, is based precisely upon the fact of the initial presence of this basophilic cell (primary 'lymphocyte' of Maximow), from which first develop erythrocytes and subsequently, from a similar cell, granular leukocytes. In other words the theory holds that the first leukocytes ('lymphocytes') precede in development the first erythrocytes, just as described for the chick by Sabin.

To return to our human embryo, one more point calls for further consideration: This embryo gives the combination of unusually large and numerous aortic cell-clusters (essentially blood-islands) and absence of a yolk-sac. This association may be simply fortuitous; but there may possibly exist a causal connection. It seems reasonable to suppose that when the yolk-sac endothelium was early incapacitated for hemogenic function due to the compression of the sac between the amnion and the chorion, resulting in disintegration, an extra hemopoietic burden was passed on to the aorta. This portion of the early hemogenic tissue may have been stimulated to compensatory hemopoietic activity in lieu of that of the yolk-sac.

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THE USE OF SANDPAPER IN THE PREPARATION OF HISTOLOGIC GROUND SECTIONS OF HARD SUBSTANCES

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In the microscopic study of specimens of compact bone, teeth, shells, hard roots, hard plant stems, etc., the technician is often confronted with the very tedious and time-consuming process of grinding and honing in accordance with present methods.

The technique herein described was devised by the author to prepare thin microscopic sections of a certain very dry, hard and brittle plant stem. Sections ground and honed by present methods required hours for their production and ultimately contained little or no cork and were in most cases too thick and irregular for photomicrography. Clogging of the surface of the water hone, burning on the lathe, warping of the section by alternate wetting and drying, general faulting and fracturing of sections, are obstacles very discouraging to the beginner and require the skill of the initiated to be overcome.

By the introduction of sandpaper in ground-section technique, the time required to obtain thin, complete, workable sections was reduced to about one-fourth. The technique, of course, is not limited to botanic research, but is applicable to all lines of histologic work in which hard substances are to be studied.

THE TECHNIQUE

A characteristic portion of the specimen is exposed by a saw cut made with a jeweler's saw. The cross, longitudinal, tangential, or oblique cut is previously determined in accordance with the contemplated study. The exposed surface is then examined by means of a magnifier to ascertain if the required detail is

present. The object is clamped in an ordinary carpenter's wood clamp or a small vise and a section 1 to 3 mm. thick removed by saw cut. Great care is taken in sawing off this coarse section, the blade of the jeweler's saw always being kept parallel to the exposed surface of the section. Manipulation of the saw blade must be steady and light. With a little practice very thin coarse sections can be obtained, their relative thickness, of course, lessening the amount of subsequent grinding. Specimens presenting exceptional difficulties to sawing may sometimes be chipped or fractured and then small thin bits selected for grinding.

The next step is that of cementing the coarse section to a microscope slide preparatory to grinding. After numerous substances were tried, shellac was found best adapted for this purpose. Rather thick heavy slides, 1 inch x 3 inches, were selected, washed in alcohol to remove possible grease, and dried. The coarse section is cemented near one end so that the slide can be firmly grasped and the index-finger pressed over the back of the section while grinding, insuring uniform distribution of pressure over the section. A pinch of dry scale orange shellac is placed on an old spoon (tea) and carefully heated just to and not beyond its melting-point. The melted shellac is then carefully poured around the coarse section, which must be held firmly against the glass to prevent the shellac from flowing under the section and raising it, thereby causing irregularities in grinding. Hot shellac sets very rapidly and the preparation is ready for grinding on the sandpaper in five minutes.

Grinding is accomplished entirely on sandpaper of different grades of coarseness, and the section is never dipped in water or oil as in present methods. Flint, sand, emery, or carborundum papers are selected according to the hardness of the material to be ground. The sand (flint) paper used was of following grades, Nos. 2, 1, 00, 0000. Sheets, 10 x 12 inches, were cut into pieces 3 x 5 inches and were held over a smooth, hard wood block, 3 x 4 inches, while grinding. Brittle substances grind best on No. 00, using a light touch. Tougher substances can be ground safely and more rapidly on Nos. 2 and 1. The index-

finger is placed on outer part of slide (outer third) directly opposite to the specimen, so as to insure uniform pressure to all parts of the coarse section, and the slide is moved with a quick, uniform, easy swing in an elliptical direction over the sandpaper surface. Particles must frequently be jolted off the surface to prevent scratching furrows. As soon as a paper becomes clogged or worn out in its entirety, it is discarded for a fresh piece. Old sheets are used in grinding prior to polishing, and some specimens even polish readily in their own dust on used papers. As soon as the first surface is ground true, it must be finished on No. 0000. Two pieces of this grade are rubbed faces together to remove large particles (to prevent scratching), and after this final grinding on No. 0000, the section is ready for polishing. The ground surface is polished by rubbing on the back (smooth side) of a piece of sandpaper, the paper pulp constituting the buffing surface. Care must be taken to have no flint particles on this surface. Final polishing may be performed on a piece of smooth ground glass, on the palm of the hand, or on a razor strop.

After grinding and polishing one surface, the section must be removed, inverted, and recemented prior to grinding and polishing its second surface. To remove the section it is best to chip away the shellac zone and then soak the specimen in 95 per cent alcohol or methyl alcohol to soften the remaining shellac. The section may then be removed by slipping a razor blade under it and lightly lifting it off to another clean, dry slide. The polished surface is placed in contact with the second slide and the section is cemented on the outer third of slide with hot shellac in the manner given above.

In cutting down the second surface, care must be taken to grind it down in a plane parallel to the surface already completed. The precaution of preventing hot shellac from flowing beneath the specimen must again be borne in mind. Simply pour the shellac around the section's periphery, extending a shellac zone $\frac{1}{2}$ inch in width around the section to insure uniformity in grinding, as this really is a guide to prevent tapering at the edge of the specimen. Frequent measurements with the micrometer or examinations with the $\frac{1}{4}$ -inch objective are necessary at the

various stages of grinding. As the section loses its thickness, care should be increased and grinding pressure decreased. Towards completion the greatest care is necessary to prevent fracture, and it is well to examine section frequently with high-power objectives. Ultimate polishing of the second surface is performed in the manner described above, but greater care is necessary.

Removal of the thin polished section from the glass side is sometimes difficult. Chip away the excess shellac zone and submerge the slide horizontally in a Petri dish of 95 per cent alcohol. Very thin sections cannot be safely manipulated with the razor blade and sometimes require four or five hours' soaking in alcohol prior to their removal. Alcoholic stains may then be used directly, or dealcoholization followed by aqueous stains may be employed. Dehydration should be slow and the clearing and mounting in balsam with cover-glass should be performed as in the ordinary methods of technique.

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